Indian Agricultural

Research Institute, New Delhi

I.A.R.I. 6

GIPNLK—4/JDIARI/60—16-3-61—5,000

MORPHOLOGY OF THE BARK-BEETLES OF THE GENUS GNATHOTRICIIUS EICHH.

BY

KARL E. SCHEDL

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INTRODUCTION

Since the early days of forest entomology, the superfamily of Sco-
lytoidea has always fascinated the investigators working on forest in-
sects. The destructive work of some of them, in spite of their relatively
small size, and also their peculiar habits were undoubtedly the reasons
for this extraordinary interest. However, with the cultivation of such
crops as coffee, tea, and other subtropical crops these insects have
become of greater interest to the economic entomologist in general.

The literature dealing with the nomenclature and the bionomics of
species belonging to this superfamily is enormous. Several attempts
have been made to construct a classification based on morphological
characters. Other investigations were undertaken to homologize cer-
tain structures to act as a guide for the proper placing of the genera
throughout the group. In this connection it is necessary to mention
only a few authors, such as Lindemann, Eichhoff, Verhoeff, Hagedorn,
Nuesslin, Fuchs, and Hopkins. However, up to the present there is
comparatively little known in regard to the morphological, histological,
and physiological details. There has been practically nothing published
concerning the muscle structure, the respiratory system (with the ex-
ception of the number and position of the spiracles in the adults and
in a few cases in the larvae), the circulatory system, the sensory
organs, the blood, the nervous system, the metamorphosis, the his-
tology, etc.

Concerning the control of the more important primary forest pests,
hundreds of recommendations have been made by different authorities.
However, all that have been made up to the present have failed to give
satisfactory control under all conditions. The recent ideas of Seit-
ner (53), used and enlarged by the Russian investigators Golov-
janko (55) and Iljinsky (60), seem, in conjunction with more careful
forest management, to represent the most hopeful direction for future
work. Undoubtedly even these modern outlooks will require enor-
mous further work to throw light upon the laws by which bark-beetle
outbreaks are governed. After solving these problems the time will
probably come when preventive measures will replace the expensive
and often useless control methods of our day.

The following investigations are a tentative endeavor leading to
a more intensive monograph of the genus *Gnathotrichus* Eichhoff.
They have been carried out as a private study.

This first paper covers the chitinous skeleton of the adult, pupa and
larva, the structure of the digestive system and the reproductive or-
gans of the adult and larva. It is hoped later to publish two more

papers, one on the sensory and secretory organs, the muscle structure, the respiratory, circulatory, and nervous systems of the larva and imago; the other on the metamorphosis and histological investigations. Whether or not a biological study will complete the work depends upon the time at the author's disposal.

The study comprises only the North-American species *Gnathotrichus materiarius* Fitch, *sulcatus* Lec. and *retusus* Lec. The necessary material, dried and mounted adults of the two western species *Gn. sulcatus* Lec. and *retusus* Lec., was kindly provided the Dominion Entomological Branch from the Canadian National Collection in Ottawa. For the adults, pupae and larvae of *Gnathotrichus materiarius* Fitch, I have to thank Mr. L. J. Simpson, of the Dominion Entomological Laboratory, in Fredericton, N. B. All the necessary slides were prepared by the author. The specimens were dissected under water and the mounts imbedded in euporal. The drawings are all by the author, and were done with the aid of the camera lucida using transmitted light.

Attempts to obtain larvae and pupae of the western species were unsuccessful and therefore the discussion of the larval and pupal characters are based on material of *Gn. materiarius* Fitch only. A supplement on this account will be published in another paper.

ABSTRACTS OF THE LITERATURE UP TO DATE

A. THE GENUS

1868. EICHHOFF, W.(3).

Original description of the genus:

Tarsorum articulis tribus primis simplicibus. Antennarum funicolo 5-articulato, capitulo distincte triannulato. Ligula parte fulcrali angustior. Palpi labiales articulis primo et secundo subeaqualibus, simplicibus, tertio minimo Maxillarum mala apice rotundata, setis falcatis densissimis ciliata, palporum articulo primo majore obconico, secundo minore subquadrato, tertio cylindrico elongato.

With respect to the position of the genus *Gnathotrichus* in the family *Scolytidae*, Eichhoff states:

Die Gattung lehnt sich durch die Form der Arten und dichte Bewimmerung der Maxillarlappen auf der einen Seite an die Gattung *Xyleborus*, auf der anderen an *Corthylus* und *Pterocyclon* an.

1876. LECONTE, J. L., and HORN, H. G. (9).

Leconte, knowing of the new genus *Gnathotrichus* Eichh., still places the species of this genus under *Pityophthorus* Eichh. However, he subdivided the genus into subgroups, the first of which comprised the species of the present genus *Gnathotrichus* described at his time.

1878. EICHHOFF, W.(11).

In the *Tomicini*, Eichhoff placed the Genus *Gnathotrichus* in his Section II, *Xylophagi*, subfamily *Xyleboridae*. The revised description of the genus as it was given on page 405 is:

Mentum oblongum, versus basin fortiter angustatum, post medium lateribus profunde sinuatum, et iterum versus apicem subdilatatum, apice rotundato; ligula linearis longa post medium menti inserta, versus apicem subdilatata, apice emarginata, angulis utrinque pilis longis munita. Palpi labiales valde elongati, articulis 1 et 2 longis, aequalibus, 3° parvo. Maxillae mala lata rotundata, pilis subtilibus longis intus ciliata, apice toto setis densissimis coactis cincta. Palpi maxillares articulis magnitudine gradatim decrescentibus, ultimo striis longitudinalibus obscuris notata. Antennae funiculo 5-articulato, articulo hujus 1° crassiusculo, bulbiformi, sequentibus multo minoribus, transversis, crassitie crescentibus, capitulo subgloboso, toto corneo, 3-articulato. Prosternum processu vix ullo. Episterna metathoracis a margine sinuato elytorum plane obtecta. Tibia lineares, extus remote denticulatae, apice truncatae. Tarsi haud recepti, articulis 1, 2, 3 aequalibus.

1883. LECONTE, J. L., and HORN, H. G.(13).

The authors placed *Gnathotrichus* Eichhoff in their key to the genera in the subfamily *Scolytinae*, the Tribe *Tomicini* and Group *Corthyli*. In the group it was separated from *Corthylus* and *Monarthrum* by its five-jointed antennal funicle and from *Pityophthorus* and *Hypothenemus* by the fringed antennal club and the "outer part of the funicle very short" respectively.

1895. BLANDFORD, W. F. H.(24).

Blandford placed *Gnathotrichus* in his subgroup V *Pityophthori* which comprises the genera *Styphlosoma* Blandford, *Dendroterus* Blandford, *Pityophthorus* Eichh. and *Gnathotrichus* Eichh. He regarded *Gnathotrichus* as standing midway between *Pityophthorus* and the *Corthyli*.

The author felt himself that the first two genera of this subgroup have very little in common with the latter two; they were included in this subgroup more on account of the difficulty of placing them elsewhere.

1909. SWAINE, J. M.(40).

Only references to literature.

1910. HAGEDORN, M.(42).

References only.

1910. HAGEDORN, M.(41).

Based on the characters of the mouthparts, Hagedorn placed the genus *Gnathotrichus* in his subfamily *Saetidentatae*. His description is as follows:

Kaukante des Mittelkiefers mit Borsten besetzt.

Unfortunately he has, like other investigators, overlooked the long slender hairs of the lacinia Therefore he misplaced the genus, which would, according to his interpretation of the characters used, fall in the subfamily *Mixtodentatae*.

1915. HOPKINS, A. D.(48).

The author placed *Gnathotrichus* in his subfamily *Corthylinae*. No details.

1918. SWAINE, J. M.(49).

The author placed the genus *Gnathotrichus* in his subfamily *Ipinae* in one group with *Conophthorus* Hopk., *Pseudopityophthorus* Sw. and *Pityophthorus* Eichh. The latter is separated from the rest of the *Ipinae* by the following characters:

Eyes not divided, antennal funicle 5-segmented, fore tibia more strongly widened, body nearly glabrous, pronotum with numerous asperities in front, the pronotum margined on the caudal border, and the metaepisternum largely covered by the elytra.

Gnathotrichus was distinguished from the other genera of this group by:

The mouthparts as seen from below rather sparsely clothed with slender hairs, the maxillary lobe pilose, body slender, very smooth, punctures and pubescens nearly obsolete except on the declivity; the pronotum closely but freely asperate in front, with an acute, arcuate, transverse, short carina at the summit, which is before the middle.

No generic description given.

1922. BLACKMAN, M. W.(50).

Characters used by earlier authors were applied in placing the genus. The arrangement is similar to that of Swaine (49); but the author did not use Swaine's character " mouthparts densely covered with hairs."

1928. BLACKMAN, M. W.(59).

The author uses the same characters as Swaine in separating the genus *Gnathotrichus* Eichh. from the rest of the *Pityophthorinae*. He regards the genera *Conophthorus* Hopkins, *Myeloborus* Blackman, *Pityophthorus* Eichhoff, *Pityoborus* Blackman, *Pityophilus* Blackman, *Pseudopityophthorus* Swaine and *Gnathotricus* Eichhoff as a compact division of the *Ipinae*.

B. GNATHOTRICHUS MATERIARIUS FITCH

1859. FITCH, ASA (1).

Original description:

Pine Timber-Beetle. *Tomicus materiarius*, new species. In the interior of
the sap wood, mining slender straight cylindrical burrows in a transverse
direction, parallel with the outer surface, from which very short straight
lateral galleries branch off at right angles above and below; a rather
slender cylindrical black shining bark-beetle, 0.15 long, with pale dull
yellow legs and antennae, the fore part of its thorax and of its
wing covers tinged with reddish yellow, the thorax equalling two-thirds
the length of the wing covers, with a small elevated tubercle in the
middle, forward of which it is rough from minute elevated points; the
wing covers with rows of minute punctures, their tips rounded, the upper
part of the declivity with a shallow longitudinal depression or groove
along the suture, forming a slight notch.

The insects belonging to the genus *Tomicus* and kindred genera of the same
family by their habits divide themselves into two distinct groups. The
larger portion of them reside in or immediately beneath the bark of
different trees and are currently termed bark-beetles. But this designation
is inappropriate for another portion of them which dwell in the interior
of the wood, and there excavate their galleries. The name timber-beetles
appears to be the most appropriate for these. Another point in which,
from the observations of M. Perris, these two groups appear to differ
in a remarkable manner, is the relative numbers of the two sexes. With the
bark-beetles there are commonly several males in company with but one
female, and the former appear to perform the chief part of the labor in
the excavation of their galleries. With the timber-beetles, on the other
hand, the females are the most numerous, and probably mine their galleries
without any assistance from the other sex. M. Perris states of one of
the species, that upwards of fifty females were met with in the burrows
they had excavated, without a single male being found there.

It is the habit of these timber-beetles to penetrate the tree in a straight
line, passing inwards through the bark and into the sap wood to a depth
of from half an inch to two inches, and then abruptly turning they extend
their burrow in another straight line parallel with the outer surface and
at right angles with the fibres of the wood, for the length of two to six
inches. The only instance in which the burrow of the species now under
consideration has come under my notice, was recently, in a billet of stove
wood, which unfortunately did not contain the extreme end of the gallery.
The annexed cut is an exact representation of this burrow, in which
a live and dead beetle were found, both of them females, and the only
specimens of this species which have come under my observation. The
transverse burrow was excavated in the sap wood at a depth of half
an inch from its outer surface. Near its middle it was crossed by another
perforation extending from the outside directly towards the heart of the
tree, which is indicated by a black dot in the figure; and at this point the
burrow curved slightly outwards toward the exterior surface, as repre-
sented in the section above the principal figure in the cut; and at its end
on the left where it passed out of the billet of wood, it commenced
curving inwards towards the heart of the tree. Twelve lateral burrows

of the same diameter as the transverse one extended upwards and two downwards, as shown in the figure, all of the same length, each one having been excavated probably by a single larva. The gallery of our insect thus differs widely from that of the European species (*T. eurygaster* Erichson) which mines in the interior of the pine, which has no lateral burrows branching off from it.

The presence of these timber beetles in the wood can be distinguished from those which mine under the bark, by the little piles of sawdust which they throw out at the mouth of their burrows, this dust being so much more white and clean, and not composed in part of the brown or rust-colored particles of gnawed bark which are intermixed with the dust produced by the bark-beetles.

In addition to the short description of this beetle which is given above, it may be observed that the head is finely punctured, the punctures on the face giving out small pale yellowish hairs, whilst those on the vertex or crown are destitute of hairs, and there is a slight transverse elevation of the surface between the face and the vertex, from which an elevated smooth line extends backwards along the middle of the vertex. Thorax, when viewed from above, with its base transverse and rectilinear, its basal angles rectangular, its opposite sides parallel for a distance equalling the length of the base, and from thence rounded in a semicircle at its anterior end; its surface anteriorly with minute asperities, which, viewed vertically, appear like fine transverse wrinkles; its basal half with very minute punctures, and in its center a small transverse tubercle. Wing covers with fine shallow punctures in rows; the upper part of the apical declivity moderately depressed in the middle, producing a slight concavity in its outline when viewed from above anteriorly, the suture not elevated in this depression, but showing a slightly impressed line along each side; the hind end bearded with hairs similar to those upon the front. Under side black, the legs and antennae pale dull yellow.

1868. ZIMMERMAN, C.(4).

In the " Synopsis of the *Scolytidae* of America North of Mexico " the author placed *materiarius* Fitch in *Crypturgus* Erich. Distribution: North Carolina, and from Maine to Canada.

1868. EICHHOFF, W.(3).

Gnathotrichus corthyloides[1]: Valde elongatus, cylindricus, subopacus piceus, elytris basi dilutioribus, antennis pedibusque ferrugineis, thorace elongato cylindrico, antice asperato, disco subnodoso, postice omnium subtilissime vage punctulato, elytris subtiliter transversim aciculatis, subtilissime seriatim punctatis, declivitate postica convexiuscula, utrinque nodulo longitudinali a sutura remoto ornata. Long. 1⅓ Lin.   Patria: America borealis, Carolina.

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[1] "Ich vermuthe, dass *Gn. corthyloides* m. identisch ist mit *Crypturgus materiarius = Tomicus materiarius* Fitch (Noxious Ins. New York II. No. 24, 246), in der soeben von Mr. Leconte zum Geschenk erhaltenen ' Synopsis of the *Scolytidae* of America North of Mexico.' "

1869. PACKARD, A. S.(5).

P. 493:

A species, probably the *Cryphalus materiarius* of Fitch, has been found by Mr. Huntington, of Kelly's Island, to bore into empty wine casks and spoil them for use.

1876. LECONTE, J. L., and HORN, H. G.(9).

Pityophthorus materiarius Fitch: Canada to Texas. Synonyms: *Tomicus materiarius* Fitch, *Crypturgus materiarius* Fitch (Zimmerman), *Gnathotrichus corthyloides* Eichh.

1877. PROVANCHER, L'ABBÉ L.(10).

The author placed *Gn. materiarius* in *Gryphalus* Er. Found in red pine (le pin rouge). Rare.

1878. EICHHOFF, W.(11).

The description of *materiarius* Fitch given by Eichhoff in his Ratio Tomicinorum is by far the most correct although it was published 50 years ago. Therefore it seems to be necessary to quote it here:

Linearis, cylindricus, nigro-piceus, subopacus, parce pilosellus, thorace elongato, anterius subtiliter rugoso-exasperato, posterius laevi, elytris basi dilutioribus, vix conspicue seriatim aciculato-punctulatis, apice rotundato, integro. Long. 3-3.2 mm.

Staturem fere et habitum coleopterorum ex genere *Pterocyclon* (*Corthylus fasciatus* Er.) exhibens, sed antennis aliter constructis. Caput deflexum, nigrum, subnitidum, fronte depressa, parce subtiliter punctata, linea media subelevata, laevi; pilis parcis, longioribus, adspersa, in margine antico non ciliato, ore inde denudato. Oculi oblongi, antice sinuati. Antennae ferugineo-testaceae, capitulo suborbiculari, compresso, subinfuscato, nitido, utraque pagina suturis duabus arcuatis notato, articulis subaequalibus. Prothorax latitudine amplius, dimidio longior, cylindricus, basi truncatus, lateribus rectis, parallelis, apice obtuse rotundatus, angulis posticis (desuper intuenti) acute rectis; supra valde cylindrice convexus, piceus, dorso ante medium lineola transversa, elevata, notatus, anterius dilutior, subrufescens, rugis imbricatis subtiliter exasperatus, tenuissime pubescens, posterior glaber, subnitidus, laevis, imo vero oculo arcute armato, omnium subtilissime parce punctulatus. Scutellum piceum, sat magnum, triangulare, nitidum laeve. Elytra cylindrica, latitudine thoraxis et illo fere tertia parte longiora, basi truncata, humeris vix elevatis subrotundatis, lateribus rectis, a basi ad medium et ultra, post medium ad apicem fortiter rotundata; supra cylindrice convexa, nigro-piceą vel brunneo-testacea, basi dilutiora, subnitida, versus apicem pilis paucis, seriatis adspersa, laevia, imo vero subtilissime lineato-punctato, interstitiis latissimis, transversim subtilissime aciculata strigulata, absque stria suturali; declivitas apicalis convexe rotundata, declivis, in singulo elytro tuberculo obsoleto, parum elevato, a sutura remoto, notata; margo apicalis communiter obtuse rotundatus. Corpus subtus nigro-piceum, cerebre subtiliter punctulatum, glabrum. Pedes ferrugineo-testacei, tibiis angustis, parum compressis, antrorsum vix dilatatis, tarsis testaceis.

Patria: America borealis (Carolina, Canada).

1881. PACKARD, A. S.(12).

The author does not bring out new facts but repeats the statements made by Fitch (1) and Perris. Also he mentions again the fact given in his " Guide to the Study of Insects." Nomenclature: *Pityophthorus materiarius* Fitch.

1886. SCHWARZ, E. A.(14).

Remarks on North American *Scolytids*:

Dr. Packard in his guide, p. 493 (see also Bull. 7, U. S. Ent. Comm., p. 174) states that " a species, probably the *Cryphalus materiarius* of Fitch, has been found . . . to bore into empty wine casks and spoil them for use." This is undoubtedly a confusion of species, as *C. materiarius* lives in pine trees. The species in question was probably *Xyleborus fuscatus,* which, in my experience, bores in several kinds of deciduous trees.

1890. SCHWARZ, E. A.(16).

Mr. Schwarz also stated that upon examination of about one hundred and fifty specimens of the common *Tomicus materiarius* Fitch (now *Gnathotrichus materiarius*) he had failed to find any males among them. In fact, the male sex appears to be never described. He alluded to the rarity of, and difficulty in finding, the males of most species of those *Scolytid* beetles which bore into the solid wood, because the males never leave the burrows.

Mr. Schwarz found *Pinus inops* as a host tree of *Gnathotrichus materiarius* Fitch.

1890. PACKARD, A. S.(15).

The author repeats nearly literally the statements of Fitch (1). No new facts.

1893. HOPKINS, A. D.(17).

Gnathotrichus materiarius Fitch. Timber-beetle. Enters green sap-wood at base stumps of dying trees. Causes " pin holes," " bluing," hastens decay. Infests pine.

Adults, May 8, July 13, October 15, May 3, November 7. Wood, Hampshire, Marion, Monongalia counties, West Virginia.

Enemies: *Hister parallelus* Say.

1894. HOPKINS, A. D.(20).

Gnathotrichus materiarius Fitch. Male = description of female. Female new. Antennae with long hairs and bristles as in *retusus.* Head smooth and sparsely punctured. Additional. Male head with elongated longitudinal elevation in front, ending in an acute point just above base of mandibles.

1895. BLANDFORD, W. F. H.(24).

Only references to literature.

1895. HAMILTON, J.(23).

Gnathotrichus materiarius, not rare, pine.

1897. HUBBARD, H. G.(26).

Hubbard, like the first author, states that *Gnathotrichus materiarius* is an ambrosia beetle; that means that its main food consists of fungus mycelium. The latter is always abundant in the tunnels.

1899. HOPKINS, A. D.(27).

Gnathotrichus materiarius Fitch. Very common in sap-wood of dead and dying pine and spruce trees, logs, and stumps; widely distributed.

Hister parallelus Say was found with *Gn. materiarius* in scrub pine wood. Kanawka Station.

1901. FELT, E. P.(28).

Taken from white and pitch pine, common.

1904. HOPKINS, A. D.(31).

The eastern pine wood stainer. *Gnathotrichus materiarius* Fitch. Excavates several branching galleries from a single entrance burrow, the broods living in short side chambers in sap-wood and heart-wood of injured, dying, and recently felled pine and spruce. Eastern United States and Canada. Very common and injurious.

1905. HOPKINS, A. D.(34).

The author describes a new species of *Gnathotrichus*, namely *nitidifrons* from Mexico. In a remark he mentions the near relationship to *materiarius* Fitch. and gives the range of the latter in pines as from Maine to Florida and Texas and in Picea from Maine to the higher mountains of North Carolina.

1905. GARMAN, H.(33).

Garman, in describing damages caused by *Monarthrum fasciatum* and *mali,* comes to the conclusion that those injuries mentioned by Packard (5) to wine casks are most probably the same.

1905. CURRIE, R. P.(32).

Copy of Hopkins, A. D.(17).

1906. FELT, E. P.(35).

No new data. Eastern pine wood stainer.

1907. FALL, H. C., and COCKERELL, T. D. A.(36).

Gnathotrichus materiarius Fitch. Cloudcroft (Viereck).

1909. SWAINE, J. M.(40).

References to literature only.

1910. HAGEDORN, M.(41).

References only.

1918. SWAINE, J. M.(49).

Host trees: Eastern pines, spruces, and eastern larch.

1922. BLACKMAN, M. W.(50).

Author found it in only one locality in the Mississippi region (Agricultural College, loblolly pine). Otherwise it was found associated with *Platypus flavicornis* Fabr., *Ips calligraphus* Germ., and the clerid *Thaninisimus dubius* Fabr. Distribution: Eastern Canada, eastern United States, as far south as Texas and Florida. Host trees: Pines, spruce and larch. In Mississippi, in loblolly pine.

C. GNATHOTRICHUS RETUSUS LEC.

1868. LECONTE, J. L.(2).

Original description:

Cryphalus retusus. Cylindrical, slender, blackish-brown; base of elytra paler; antennae and feet yellowish; head prominent, convex, subcarinated, shining sparsely punctured; prothorax nearly one-half longer than wide, sides slightly converging from the base and feebly rounded, tip strongly rounded, surface rough and sparsely hairy before the middle, granules tolerably coarse near the tip, behind the middle sparsely punctulate; elytra very finely rugose and distantly punctulate in rows, and with a few very long hairs behind the middle, posterior declivity with a deep depression along the suture, limited each side by a longitudinal obtuse elevation, bearing on its highest portion a few very fine denticulations; suture not elevated. Long. 3.5 mm.

Collected in the coast region of California and Oregon by Doctor Horn. This species has the same form and sculpture as *C. materiarius,* but is larger and readily distinguished by the different sculpture of the posterior declivity of the elytra.

1876. LECONTE, J. L., and HORN, H. G.(9).

Pityophthorus retusus Lec.: California, Oregon, Vancouver Island. Leconte doubted his formerly described *sulcatus* Lec. and is of the opinion that this is really the male of *retusus.*

1878. EICHHOFF, W.(11).

Quotes Leconte's description.

1893. HOPKINS, A. D.(17).

Gnathotrichus retusus Lec. Timber-beetles. Enters sap-wood. Causes pin holes and bluing. Infests white pine, also other pines. Adults from Virginia near West Virginia line, October 21. Adults dead in white pine wood, August 29. Monongalia county and Virginia. The only record of *retusus* in the eastern United States.

1894. HOPKINS, A. D.(20).

In Leconte and Horn "*Rynchophora* of North America," the description of male is that of female; female description is of male. Additional: Male club of antennae with a few short, stiff hairs. No long bristles. Head with a longitudinal elevation

in front. Female antennae with a long bristle rising from the anterior edge of each joint of the funiculus, and the first and second joint of the club; also with a few long hairs, all curving upwards.

1906. FELT, E. P.(35).
Only reference to Hopkins (17). '

1907. FALL, H. C., and COCKERELL, T. D. A.(36).
Gnathotrichus retusus Lec. Gallinas Cañon (Doctor Snow).

1909. SWAINE, J. M.(40).
References to literature only.

1910. HAGEDORN, M.(42).
References only.

1914. SWAINE, J. M.(47).
Swaine brings a short discussion of the habits of *Gn. retusus* Lec. and *sulcatus* Lec. In general it can be concluded that these habits are very similar to those of *Gn. materiarius* Fitch described by earlier authors. The author says:

The adult beetles excavate cylindric tunnels, about the diameter of a small pencil lead, from four to about six inches into the wood. The entrance tunnel, entering usually in the depth of a bark-fissure, passes directly through the bark and into the wood for from one to two inches; there branching takes place in a somewhat irregular fashion, though all parts of the set of tunnels extend in the same horizontal plane. Usually one long side-tunnel is cut shortly within the bark, parallel to the wood surface. The meal-like boring-dust and excrement are extruded through the entrance hole. Along the inner tunnels above and below, the females cut cup-like niches and deposit an elongate egg in each. The larva which hatches from the egg lengthens the niche in which it finds itself into a short tunnel or larval-cradle, slightly more than its own length when full grown, and transforms therein to the pupal stage, with its head toward the egg-tunnel. The pupa transforms to the adult in the cradle. The chief food of the larva, and an important food of the adult, is a peculiar fungus called Ambrosia, which grows in a dense glistening layer upon the walls of the tunnels and cradles. It penetrates the cut wood-cells and grows for a considerable distance along the vessels, but is entirely saprophytic in its relation to the wood. The walls of the tunnels are stained black for a millimeter or more in thickness. These, small, black, round, branching tunnels in the wood are characteristic of the Timber-beetles or Ambrosia-beetles.

The winter is passed by parent adults in the tunnels and cradles, and pupae and larvae of various sizes in the cradles. Apparently work is continued in these tunnels in the spring; and new tunnels are started by the young adults. A second brood appears and starts fresh tunnels early in August.

A considerable amount of injury is caused by these pine hole borers, and they are likely to become more numerous in the future, as cutting becomes more extensive. They breed in all dying trunks, and recently cut logs and stumps; never in dead and dry wood, and seldom, perhaps never, in perfectly healthy trees. The timber-beetles are particularly injurious in the west to fire injured timber. As a control measure it is suggested to pile the logs in a way that they may dry out quickly or when possible to place them in water.

1918. SWAINE, J. M. (49).
No new data concerning the description and biology. Host trees: Western hemlock, Douglas fir, western yellow pine. Distribution: Generally distributed through southern British Columbia and southward.

1922. HOPPING, R. (51).
Hopping gives for *Gn. retusus* Lec. the following Host trees: *Pinus ponderosa* Laws, *Pinus lambertiana* Dougl., *Pinus jeffreyi* Oreg. Com., *Pinus contorta* London, *Pseudotsuga taxifolia* Britt., and *Tsuga mertensiana* Bong.

D. GNATHOTRICHUS SULCATUS LEC.

1868. LECONTE, L. J. (2).
Original description:
Cryphalus sulcatus. Form, size and sculpture precisely the same as in *C. retusus,* except that the front is divergently aciculate, and the occiput is sparsely punctured; the elytra are similarly punctulate in rows, but the general surface is more distinctly and densely rugose; the retuse elevation of the posterior declivity of the elytra is but slightly prominent, and not denticulate; the hairs behind the middle of the elytra are less numerous. Long. 3.5 mm.
One specimen from the coast region of middle California was given me by Doctor Horn. The color is paler than that of the three specimens of *C. retusus* now before me, being yellowish-brown, with the base of the thorax and the sides and tip of the elytra darker. Probably more mature specimens would be darker; it is perhaps the female of the preceding, but having failed to find any sexual characters in *C. materiarius,* I am not warranted at present in so regarding it.

1876. LECONTE, J. L., and HORN, H. G. (9).
Pityophthorus sulcatus Lec. See under *retusus* Lec.

1878. EICHHOFF, W. (11).
Quotes Leconte's description.

1904. HOPKINS, A. D. (31).
Western hemlock wood stainer. *Gnathotrichus sulcatus* Lec. Excavates numerous branching galleries from a central burrow, the broods living in closely joined side chambers; in the sap-wood and heart-wood of western hemlock, Douglas spruce, giant arbor vitae, and fir. California to northern Washington; common in hemlock.

1905. HOPKINS, A. D.(34).

The author examined one specimen from Chaleo and another from Michocan, Mexico, and suggested that Blandford's *Gnathotrichus consentaneus* is identical with *sulcatus* Lec.

1905. CURRIE, R. P.(32).

Copy of Hopkins, A. D. Fir is replaced by lowland fir.

1907. FALL, H. C., and COCKERELL, T. D. A.(36).

Gnathotrichus sulcatus (Hopkins MS.). —— Beulah (Skinner).

1909. SWAINE, T. M.(40).

References to literature only.

1910. HAGEDORN, M.(42).

References only.

1914. SWAINE, J. M.(47).

See *retusus* Lec.

1918. SWAINE, J. M.(49).

No new data concerning the description and the biology. Host trees: Grand fir, western hemlock, Douglas fir, western white pine. Distribution: Generally distributed throughout southern British Columbia, extending southwards. In sap-wood and heartwood of dying and recently killed trees, and more rarely in those apparently sound.

1922. HOPPING, R.(51).

According to the author *Gn. sulcatus* breeds in the following host trees: *Pinus monticola* Dougl., *Abies concolor* Parry, *Abies magnifica* Murr., *Abies grandis* Lindl., *Pseudotsuga taxifolia* Britt., and *Tsuga heterophylla* Raf.

SYNONYMA

A. Gnathotrichus materiarius Fitch

Tomicus materiarius Fitch (Fitch, Schwartz, 1890, Packard, 1890).
Crypturgus materiarius Fitch (Zimmerman, Packard, 1869).
Gnathotrichus corthyloides Eichh.
Pityophthorus materiarius Fitch (Leconte, Packard, 1881).
Cryphalus materiarius Fitch (Provancher).

B. Gnathotrichus retusus Lec.

Cryphalus retusus Leconte, 1868.
Pityophthorus retusus Lec. (Leconte, 1876).

C. *Gnathotrichus sulcatus* Lec.

Cryphalus sulcatus Leconte, 1868.
Pityophthorus sulcatus Leconte, 1876.

COMMON NAMES

A. Gn. materiarius Fitch.
> Pine timber-beetle (Fitch).
> Timber-beetle (Hopkins, 1893).
> Eastern pine wood stainer (Hopkins, 1904, Felt, 1906).

B. Gn. retusus Lec.
> Timber-beetle (Hopkins, 1893, Swaine, 1914).
> Pine hole borer (Swaine, 1914).

C. Gn. sulcatus Lec.
> Western hemlock wood stainer (Hopkins, 1904).

THE CHITINOUS SKELETON OF THE ADULT

GENERAL APPEARANCE, VESTITURE, COLOR, AND SIZE

The general form of all three species is slender in both sexes, cylindrical, with the head concealed from above by the pronotum. The pronotum is longer than wide with the sides parallel on more than the caudal half and broadly rounded in front. The elytra are slightly narrower or as wide as the pronotum, subparallel as far as the origin of the declivity, sometimes slightly tapering posteriorly; moderately broadly rounded behind.

Length and relative proportions. (Dorsal aspect).—
> *Gnathotrichus materiarius* Fitch.
>> Length of the body (elytra and pronotum; head concealed from above), 3.06 mm.
>> The body is 3.11 times as long as the width of the pronotum.
>> Width of pronotum, 0.98 mm.
>> The elytra are 1.46 times as long as the pronotum.
>> Examined specimens, 12.
> *Gnathotrichus retusus* Lec.
>> Length, 3.72 mm.
>> The body is 3.23 times as long as the width of the pronotum.
>> Width of the pronotum, 1.15 mm.
>> The elytra are 1.54 times as long as the pronotum.
>> Examined specimens, 10.

FIG. 1.—*Gnathotrichus materiarius* Fitch, adult male, lateral aspect.

An, antenna; *Ep*, epistoma; *Epl*, epipleurite; *Bpm*, epimeron; *Epst*, episternum; *Ey*, compound eye; *HL*, hind legs; *Hypl*, hypopleurite; *FL*, forelegs; *Fr*, front; *Md*, mandible; *ML*, middle legs; *Msst*, mesosternum; *Msth*, mesothorax; *Mtst*, metasternum; *Mtth*, metathorax; *Mx*, maxilla; *Pr*, pregula; *Prn*, pronotum; *Prst*, prosternum; *Prth*, prothorax; *Prct*, prescutum; *Sc*, scutum; *Sct*, scutellum; *Sp*, spiracle; *Su*, summit; *T*, tergite; *Ve*, vertex; *a*, coracoid and clavicle process; *b*, coxa; *c*, femur; *d*, tibia; *e*, tarsus; *f*, lateral wing lock; *g*, transverse impression of pronotum.

Gnathotrichus sulcatus Lec

Length, 3 59 mm

The body is 3 38 times as long as the width of the pronotum

Width of the pronotum, 1 07 mm

The elytra are 1 60 times as long as the pronotum

Examined specimens, 10
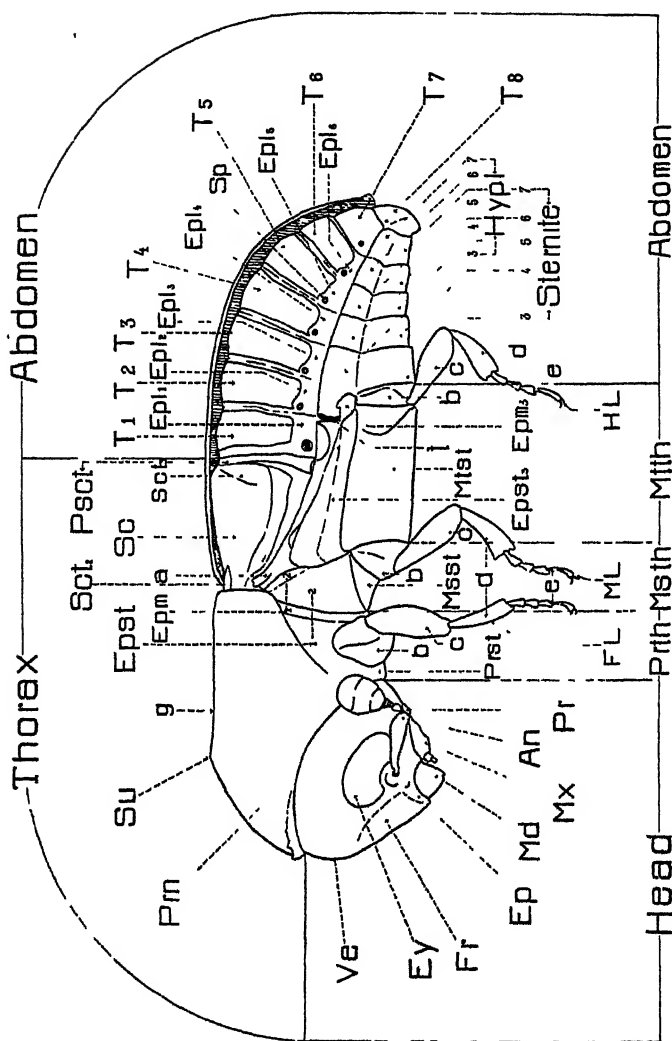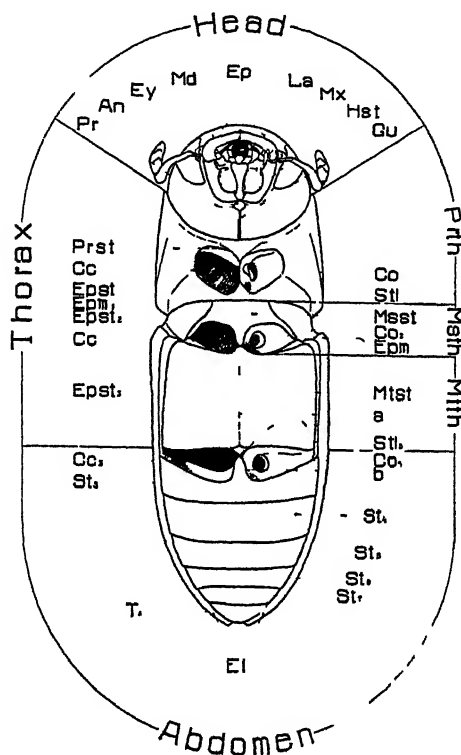

FIG. 2—*Gnathotrichus materiarius* Fitch, adult male, ventral aspect.

An antenna, *Cc*, coxal cavity, *Co*, coxa, *Ep*, epistoma, *Epm*, epimeron, *Epst*, episternum, *Ey*, compound eye, *Gu* gular area *Hst* hypostoma, *La* labium, *Mst*, mesosternum, *Msth*, mesothorax, *Md*, mandible, *Mtst*, metasternum *Mtth* metathorax, *Mx*, maxilla, *Pr*, pregula, *Prst*, prosternum, *Pth*, prothorax, *st*, sternite, *Stl*, sternellar area, *a*, median line

Color.—The color ranges from a reddish-brown to nearly black in mature specimens, it is of no importance in this genus.

Vestiture —In general it can be said that all three species are without extraordinary hair characters; few large bristles occur on the declivity. However, by careful examination under the microscope it was found that all external parts are more or less covered with fine hairs.
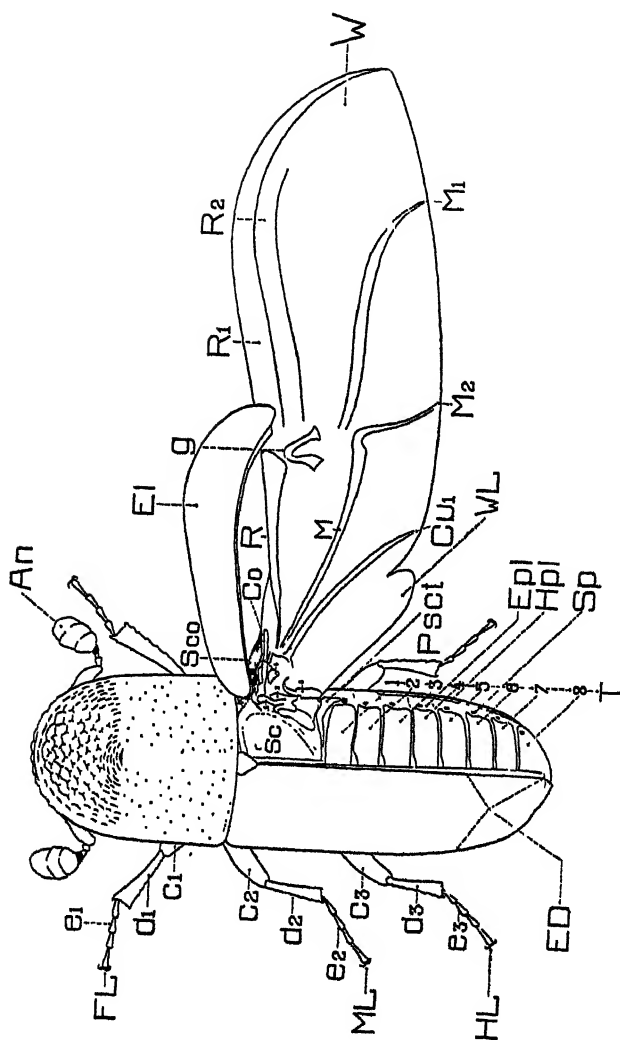
FIG. 3.—*Gnathotrichus materiarius* Fitch, adult male, dorsal aspect.

An, antenna; *Co*, coxa; *Cu*, cubitus; *ED*, elytra declivity; *El*, elytra; *Epl*, epipleurite; *FL*, fore legs; *HL*, hind legs; *Hpl*, hypopleurite; *M*, median veins; *ML*, middle legs; *Psct*, postnotum or postscutellum; *R*, radius; *Sc*, scutum of metathorax; *Sco*, subcostal vein; *Sp*, spiracle; *T*, tergite; *W*, metathoracic wing; *WL*, wing lobe; *c*, femur; *d*, tibia; *e*, tarsus; *g*, median folding hinge of wing; 1, 2, 3, 4, the four axillaries.

Sculpture.—The front and the elytral declivity are the only bearers of specific modifications. The sculpture of the pronotum and the elytra, which is very useful in distinguishing the species in many other genera of the *Scolytidae,* does not vary to any extent in this genus

Secondary sexual characters—Secondary sexual characters were found in the development of the hairs on the antennae, the number of fully developed tergites and in the number of spiracles mainly.

THE HEAD

The head capsula or cranium (figs. 4-7) is dorsally divided by the epicranial suture. The sutura fronto verticale Berlese or coronal suture (figs. 5, 6, Cos) is distinct in all three species examined. In *Gnathotrichus retusus* Lec., and less pronounced in *Gn. materiarius* Fitch, this suture and a short piece of the sutura metopica da Miall and Denny or frontal suture become elevated near the junction, forming a Y-like ridge. The slightly raised line (figs. 4, 5, a) which originates at the upper margin of the antennal groove (figs 4, 6, b, 7, c) and which is directed toward this junction may be considered a remnant of the frontal suture. These anterior remnants of the frontal suture are never connected with the posterior portion.

Front.—The area between the frontal sutures is largely occupied by the frons (figs. 4, 5, 7, Fr). The shape of the front is plano-convex; the median line is slightly raised, and there is a shallow depression on each side of the latter. The front is sculptured by scratches which radiate from the center of the anterior margin, and which extend over the entire sclerite, becoming less distinct and less dense towards the outer margin. These scratches look as though they had been made with a needle point, and therefore have been called acciculation by several authors. Scattered over the acciculate area are small but deep, sparse punctures. Bristles varying from short to moderately long occur over the entire front; most of these originate in punctures. They are more numerous in the antero-lateral corners.

Specific modifications:—

A—Acciculation strongly developed, close; front with punctures near the outer margin and antero-lateral region only, with bristles very sparse in the acciculate area (fig. 5, Ac).

Gn. *sulcatus* Lec.

AA—Acciculation weakly developed or obsolescent, more or less restricted to the median anterior area; front elsewhere punctulate, bristles more numerous.

Gn. *retusus* Lec. and *materiarius* Fitch.

Labrum, clypeus and epistoma.—The labrum and clypeus are not evident as separate sclerites. The epistoma (figs. 4, 5, 7, ep), probably also containing elements of the labrum and clypeus, is not separated from the front by a distinct suture or line. It is present as a ridge and forms the anterior margin of the front. This region is widened laterally, and is connected with an elevation which surrounds the antennal
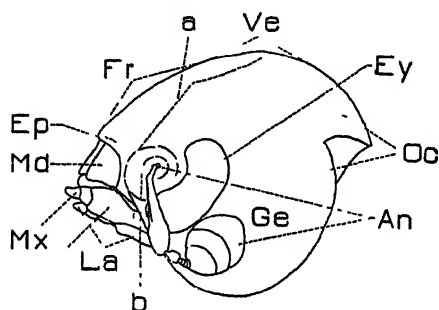

FIG. 4.—*Gnathotrichus sulcatus* Lec.: Head, lateral aspect.

An, antenna; *Ep,* epistoma; *Ey,* compound eye; *Fr,* frons; *Ge,* gena; *La,* labium; *Md,* mandible; *Mx,* maxilla; *Oc,* occipital area; *Ve,* vertex; *a,* frontal suture; *b,* antennal groove.
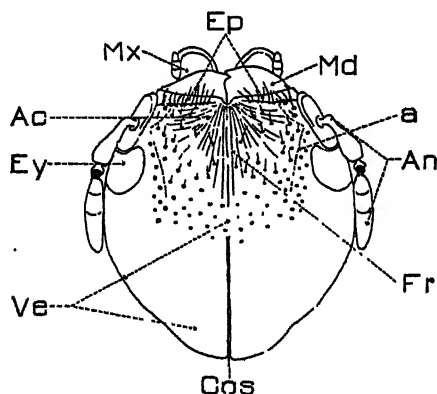
FIG. 5.—*Gnathotrichus sulcatus* Lec.: Head, dorsal aspect.

Ac, acciculation; *An,* antenna; *Ep,* epistoma; *Ey,* compound eye; *Fr,* frons; *Md,* mandible; *Mx,* maxilla; *Cos,* coronal suture; *Vc,* vertex; *a,* frontal suture.

scrobe. In the middle of the anterior margin, an evenly rounded emargination is visible which may be called serratus epistomalus (fig. 7, SE) and which corresponds to Hopkin's median impression. From the serratus epistomalus the acciculation of the front radiates. The epistoma is without sculpture and bears a row of bristles on its posterior margin. The mandibles articulate with the underside of the epistoma.

Gula—The gula is bounded by the two very closely placed gular-sutures (figs 6, 7, Gus) and widens anteriorly to form the pregula.

FIG. 6—*Gnathotrichus sulcatus* Lec . Head, ventral aspect.

An, antenna, *Cos*, coronal suture, *Ey* compound eye, *Ge*, gena, *Gus*, gular sutures, *Hy*, hypostoma, *La*, labium, *Md*, mandible, *Mx*, maxilla, *Oc*, occipital area, *Oca*, occipital apodeme, *Oct*, occipital foramen, *Pr*, pregula; *a* dorsal articulation of the mandible, *b*, ventral articulation of the mandible, *c*, antennal groove.
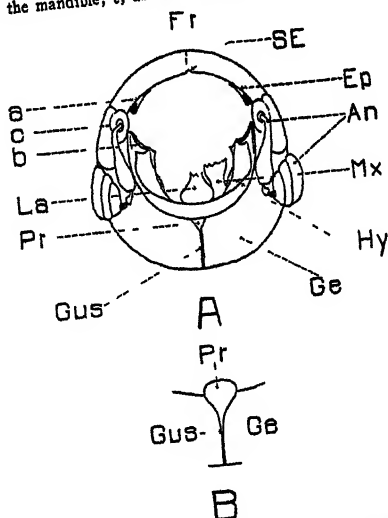
FIG. 7.—A, *Gnathotrichus sulcatus* Lec · Head, oral aspect B, *Gnathotrichus retusus* Lec : Pregula.

An, antenna *Ep*, epistoma, *Ge*, gena, *Gus*, gular sutures, *Fr*, frons, *Hy*, hypostoma, *La*, labium, *Mx*, maxilla, *Pr*, pregula, *SE*, serratus epistomalus, *a*, dorsal articulation of mandibles, *b*, ventral articulation of mandibles, *c*, antennal groove

These two distinct sutures appear to be exceptional in this family. Hopkins apparently did not find any double sutures in his investigations.

In *Gnathotrichus,* the pregula (figs. 6, 7, Pr) is always without sculpture or hairs. The very distinct specific modifications are described in the following key:

A—Pregula flat, triangular, not produced anteriorly, its anterior margin continuous with those of the gena.

<div style="text-align: right">*Gn. sulcatus* Lec.</div>

AA—Pregula convex, produced anteriorly, its anterior not continuous with those of the gena.

B—Pregula very convex, extending far beyond the genal margin.

<div style="text-align: right">*Gn. retusus* Lec.</div>

BB—Pregula feebly convex, extending slightly beyond the genal margin.

<div style="text-align: right">*Gn. materiarius* Fitch.</div>

Epicranium.—The remaining lobes of the cranium situated between the epicranial suture, the gula, and the foramen bear the compound eyes (figs. 4-6, Ey), the antennae and the articulations of the mouthparts. For merely descriptive purposes these lateral areas of the cranium have been divided into several regions. The occipital area (figs. 4, 6, Oc) surrounding the occipital foramen is not limited anteriorly in *Gnathotrichus.* However, there occur obscure lines which may be regarded as homologous with the occipital suture. The epicranium or parietals (Crampton), the gena, and the vertex do not show any sculpture which exhibits specific differences. The hypostoma (Hopkins) (figs. 6, 7, Hy), an area corresponding to the epistoma, which like the former belongs morphologically to the epicranium, is well developed.[1] It is in the form of a semicircular band and bears at its extremities the ventral articulations (figs. 6, 7 b) of the mandibles. From the oral aspect it is visible; from the ventral, it is hidden by the pregula and the gena.

Other regions, such as the pregena (Hopkins), etc., are not at all distinct or limited and are therefore of no interest in this discussion.

THE APPENDAGES OF THE HEAD

THE ANTENNAE

The antennae present good generic characters; the species modifications are less important. The sexual differences are distinct also. All the longer setae of the antennae are feathered.

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[1] The hypostoma, as the term is used here, or the ventral angles of the postgena, is the bearer of the maxillare and not the labium. A submentum, as this term was used by Hopkins in *Dendroctonus,* is not defined by sutures.

The scape (fig. 8, A, S) is slender and clavate toward the apex. Hairs and punctures are rather sparse. The scape is about as long as the funicle and the club together. The funicle (fig. 8, A, F) is
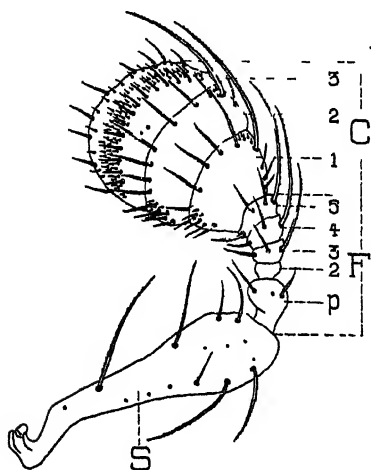
FIG. 8, A.—*Gnathotrichus retusus* Lec., adult female: Antenna, internolateral aspect.

C, antennal club; *F*, funicle; *S*, scape; *p*, pedicle; *2*, *3*, *4*, *5*, joint of the funicle; *1'*, *2'*, *3'*, joints of the club.
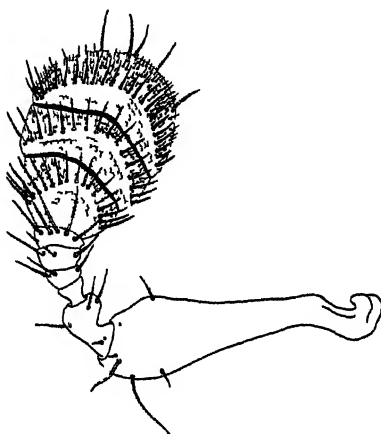
FIG. 8, B.—*Gnathotrichus retusus* Lec., adult female: Antenna, externolateral aspect.
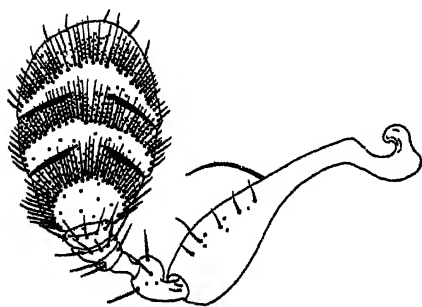
FIG. 8, C.—*Gnathotrichus sulcatus* Lec., adult male: Antenna, externolateral aspect.
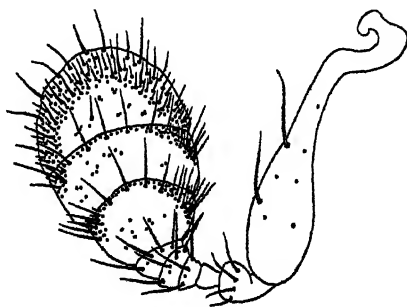
FIG. 8, D.—*Gnathotrichus sulcatus* Lec., adult male: Antenna, internolateral aspect.

five-jointed and distinctly shorter than the club. The pedicle (fig. 8, A. p) the first and longest of all joints, is as long as joint two and three together. The setae and punctures are more concentrated on the apical half of the pedicle, only two small bristles occurring near the basal articulation (fig. 8, B). The other joints decrease in

length but increase in width towards the club. All the joints bear numerous punctures and hairs except the second which has neither. The club (fig. 8, A, C) is from 1.21 to 1.35 times as long as wide, egg-shaped in outline, widest near the apex and strongly compressed. Two nearly continuous septate sutures divide the club into three joints. The first and third joints are nearly equal in length; the second is distinctly shorter. The septae are arcuate and distinctly visible from the externo-lateral aspect (fig. 8, B, C). On the interno-lateral side (fig. 8, A, D) they are indicated by single sutures. Each of the joints is covered by numerous hairs and punctures. Externo-laterally these are closely placed and arranged in arcuate rows; interno-laterally, they are sparse, and the punctures are more numerous.

The females (fig. 8, A) bear, moreover, on the interno-anterior margin of the club a few very long hairs. The anterior setae of the third, fourth, and fifth joints of the funicle are longer in this sex. These are the only external characters by which the sexes may be distinguished when the elytra are kept in the closed position.

Specific modifications:—

A—Septae in the form of continuous bands of equal width throughout, slightly less pronounced medially; externo-lateral side of the club with minute, transverse wrinkles and small punctures producing a slightly roughened surface (fig. 8, A, B).

<div style="text-align: right;">

Gn. retusus Lec.
</div>

AA—Septae wider laterally, indistinct and narrow medially; externo-lateral side of the club smooth or with very minute, sparse wrinkles; club stouter.

B—Externo-lateral side of the club smooth, interno-lateral side with numerous hairs and punctures (fig. 8, C).

<div style="text-align: right;">

Gn. sulcatus Lec.
</div>

BB—Externo-lateral side of the club with minute wrinkles, interno-lateral side with very few hairs and few punctures; club very stout.

<div style="text-align: right;">

Gn. materiarius Fitch.
</div>

THE MOUTHPARTS

The mouthparts present generic as well as specific characters. They include the mandibles, the first maxilla and the second maxillae or labium.

Mandibles.—The mandibles (fig. 9) are very much alike in all three species, so much so that it is not possible to distinguish them by mandibular characters. The shape is stout and triangular as in most Scolytidae. The apical tooth (fig. 9, a) and the subapical tooth (fig. 9, b) are well developed and separated by a deep emargination. In contrast to other genera, two median teeth (fig. 9, c) occur. The latter are rather feebly developed and the separating emargination is shallow. The molar tooth (fig. 9, d) is evenly rounded. There are one lateral and two dorsal setae (fig. 9, f, g). Other details are illustrated in figure 9. No specific differences have been found in these.
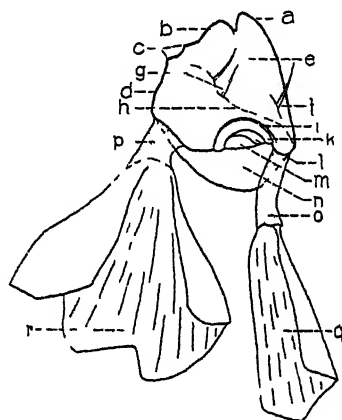
FIG. 9.—*Gnathotrichus materiarius* Fitch: Mandible, dorsal aspect.

a, apical tooth; *b*, subapical tooth; *c*, median teeth; *d*, molar tooth; *e*, dorsal area; *f*, lateral bristle; *g*, dorsal bristles; *h*, transverse ridge; *i*, anterior fossa; *k*, condyle; *l*, posterior fossa; *m*, posterior impression; *n*, condyle of ventral articulation; *o*, extensor tendon; *p*, retractor tendon; *q*, extensor disk; *r*, retractor disk

The Maxilla.—The maxillae (figs. 2, 6) are exposed on each side of the labium. Each is held in such a way that the cardo is parallel with the long axis of the head; the stipes, lacinia, and galea are at right angles to the cardo; the second and third palpial joints are slightly curved outwards. The galea and lacinia are represented by two lobes which are fused except at the apex where they are separated by a moderately deep notch. The stipes is separated from these fused lobes by a very fine, feeble suture on the outer side; on the inner side, no suture is evident. Another paper will deal with the generic differences in the maxilla of *Gnathotrichus* Eichh. and related genera. Nevertheless, it should be noted that, as far as known at present, the labium and the maxillae in the genus *Pityophtorus* Eichh. always bear at least a few feathered bristles; in *Gnathotrichus*

Eichh. these bristles are simple. This is important, as it has been seen that the character "maxilla spinose" in *Pityophthorus* Eichh. and "maxilla pilose" in *Gnathotrichus* Eichh., as used by several
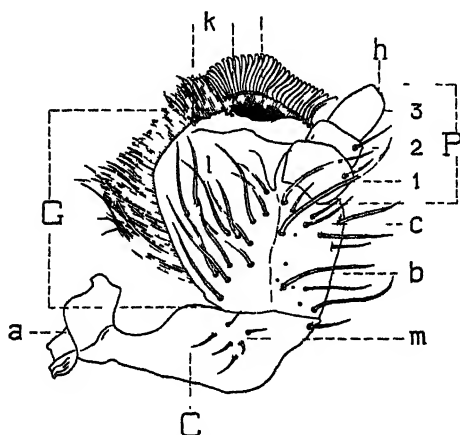
Fig. 10.—*Gnathotrichus sulcatus* Lec.: Maxilla, outer aspect.

C, cardo, *G*, galea, *P*, palpus, 1, 2, 3, first, second and third joint of the palpus; *a*, articulation of the maxilla, *b*, stipes; *c* palpiferal area, *i* anterior emargination separating galea and lacinia, *k*, dorsal setae of the galea, *l*, median setae of the galea; *m*, cardol setae.
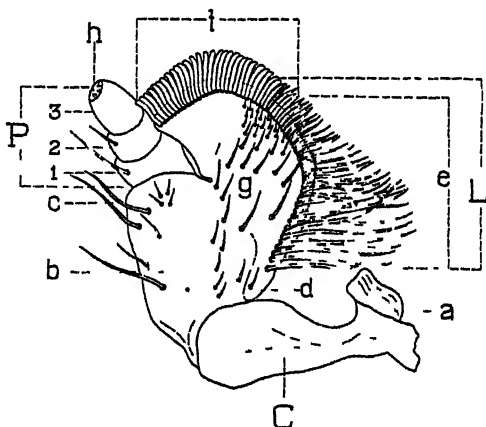
Fig. 11.—*Gnathotrichus sulcatus* Lec.: Maxilla, inner aspect.

C, cardo; *L*, lacinia; *P*, palpus; 1, 2, 3, first, second and third joint of the palpus; *a*, articulation of the maxilla; *b*, stipes, *c*, palpiferal area; *d*, subgaleal area; *e*, posterior setae of the lacinia; *f*, dorsal setae of the lacinia; *g*, median setae of the lacinia; *h*, papilla.

authors to separate *Gnathotrichus* Eichh. from the rest of the *Pityophthorinae* does not hold, as will be shown in the discussion of the lacinia and galea. The maxillae exhibit no specific differences of importance in *Gnathotrichus*. The maxillae are illustrated in figures 10 and 11.

Cardo.—The cardo (C) is similar in shape in all three species and is articulated with the ventral angles of the postgena in such a way that the maxilla can be moved laterally as well as in a dorsal-ventral plane. The longitudinal axis of the cardo and that of the stipes (b) enclose an angle of about ninety degrees or even a little less. The articulation of the stipes and the cardo is similar to that of other genera of the family. There is also an articulation between the sub-galea and the cardo. In figure 12, which illustrates this fact, the cardo and the rest of the maxilla are stretched to show the connection. The inner side of the cardo is smooth; the outer side shows from five to seven hairs which may be called the cardol setae (m).

Stipes.—On the outer side the stipes is defined as an elongate, sub-parallel sclerite; on the inner side it is fused with the lacinia. The
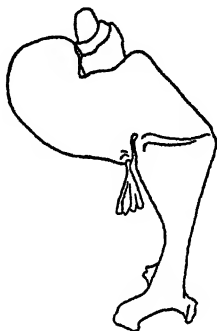
FIG. 12 —*Gnathotrichus materiarius* Fitch   Maxilla, stretched, the subgalea showing.

setae are not very numerous, about six to eight being present. These are more concentrated anteriorly near the base and near the apex. The latter, situated on the apical area of the stipes, may correspond to the palpiferal setae of some authors. The palpifer (c) being a topographical area of the stipes only, is not limited by lines or sutures.

Lacinia and galea.—The lobus internus or the lacinia and the lobus externus or the galea are largely fused to form a single large lobe. Apically they are distinctly separated by a moderately deep emargination (i) or notch. The inner free lobe is distinctly larger than the outer one. Posteriorly they are fused. It will need much further investigation to decide the exact areas of these two lobes. In the meantime it is proposed to call the inner lobe and the inner surface of the combined lobes the lacinia and the outer free lobe and the outer surface of the fused part the galea.

The lacinia bears on the anterior portion of the free dorsal margin short, stout, blunt setae (f) which are slightly incurved at their tips
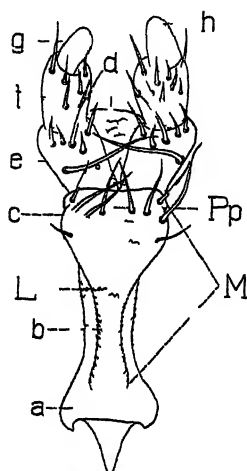
FIG 13, A —*Gnathotrichus retusus* Lec Labium ventral aspect

L ligula *M* mentum *Pp* palpifer *a* base of ligula *b* neck of mentum *c* ventral setae of the ligula *d* anterior part *f* ligula *e* first joint of palpus *f* second joint of palpus *g* third joint of palpus
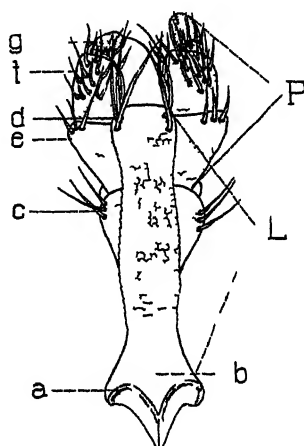
FIG 13, B —*Gnathotrichus retusus* Lec Labium, dorsal aspect

l palpus *L* ligula *a* articulation of the labium *b* base of ligula *c* dorso lateral setae of the palpifer *d* dorso anterior setae of the ligula *e f g* first second and third joint of the palpus
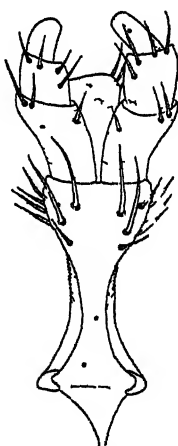
FIG 13 C —*Gnathotrichus sulcatus* Lec Labium, ventral aspect

FIG 13 D —*Gnathotrichus sulcatus* Lec Labium, dorsal aspect

These setae gradually become longer, more slender, and pointed posteriorly (e) Near the subgaleal area (fig 11 d) they are about three times as long as on the dorsal margin Besides these setae on the outer

margin of the lacinia numerous bristles (g) are scattered over the entire lobe; the surface is slightly reticulate. Basally, the united lacinia and galea end in a lobe, the subgaleal area (d), which is distinctly defined on the inner side by an impressed line. The galea bears a short row of slender setae (k) on its free dorsal margin; the surface is armed with rather sparse, long hairs (e).

Adopting the terms of other authors, it may be said the lacinia is pilose on its dorsal margin and spinose on its posterior and that the galea is spinose.

Palpi.—The palpi (P) are three-jointed. The first joint is the longest, the second and the third are subequal in length. Anteriorly joints one and two bear setae, joint three punctures only. There occur slight differences in the size and the shape of the joints in the species, but they are not distinct enough to be of importance

Labium.—The labium (fig. 13), consisting of the mentum, the ligula, and the palpi mainly, presents the most important generic and specific characters of the mouthparts.

The shape of the mentum (fig. 13, M) is similar in all three species. It is flask shaped, the palpifera always being wider than the neck (fig. 13, b) and the base of the mentum and the latter always narrower than the ligula (fig. 13, L). The basal portion of the mentum is feebly widened in *Gn. retusus* Lec. (fig. 13, A) and strongly widened in *Gn. materiarius* and *sulcatus* (fig. 13, C). In *Gn. sulcatus* and *materiarius,* the mentum and the ligula are separated by deep sutures throughout, even at the extreme base of the ligula; in *retusus* they are similarly distinct except at the extreme base before which they completely disappear. The sculpture of the mentum on the ventral side (fig. 13, C), except for a few distinct punctures, is smooth in *Gn. sulcatus*. *Gn. materiarius* is very similar but it shows slight evidences of transverse wrinkles also. In *Gn. retusus* the punctures are obsolete; the wrinkles are strongly developed and become on the neck of the mentum and the basal half of the palpifer more or less toothlike (fig. 13, A). All the setae are simple bristles (c), and there are eight to ten of these bristles on each half of the ventro-lateral side of the apical third of the palpifer. In *Gn. retusus* and *materiarius* there are ten of these bristles; in *sulcatus* eight is the usual number.

Ligula.—In this genus, the ligula (L) is much larger and more prominent than is usual; it is wider than the mentum in its basal half and is distinctly limited by sutures at the extreme base of the labium except in *retusus*. The ligula (fig. 13, L) extends in all three species a little farther anteriorly than the first joint of the palpus. Its

shape is elongate; it is subparallel with two more or less distinct contractions when viewed from the dorsal aspect. The basal portion is semicircular in cross-section, while the anterior, unfused part is strongly compressed. In *Gn. retusus* Lec., the ligula is more parallel and the contractions less distinct than in the other species.

The anterior margin is very feebly, shallowly emarginate or evenly rounded; however, this does not seem to be constant in individuals of the same species. On the ventral aspect, there is on each side near the anterior margin a row of setae (d). No specific differences have been found either in the shape or in the number of these setae which vary in number from three to seven in each row. The sculpture of the ligula on the ventral aspect in all three species is very much alike, being nearly smooth or feebly transversely wrinkled. Dorsally *Gn. retusus* shows similar transverse, toothlike wrinkles on the mentum; the basal portion only is smooth. *Gn. materiarius* and *sulcatus* have the corresponding area smooth with slight indications of transverse wrinkles on the sides.

Palpi.—The palpi are directed ventrad. Each is composed of three segments, decreasing in size toward the apex. Segments two and three bear dorsally a plush-like arrangement of hairs, while the first joint has a few scattered hairs only. Ventrally, the setae are more sparse and are intermixed with punctures on segments one and two; segment three has no setae but a few punctures.

Summary of the specific characters:—

A—Base of the mentum scarcely widened basally, fused with the ligula before the basal margin of the latter; mentum and ligula when seen from above with strongly developed, toothlike, transverse wrinkles; ligula subparallel. *Gn. retusus* Lec.

AA—Base of the mentum distinctly widened basally, extending to the basal margin of the labium; mentum and ligula when seen from below smooth or with slight indications of transverse wrinkles; contractions of the ligula well developed.

    B—Ventral side of the mentum smooth, with few punctures.

                                                          Gn. sulcatus Lec.

    BB—Ventral side of the mentum with transverse wrinkles.

                                                 Gn. materiarius Fitch.

THE THORAX

The three segments of the thorax, pro-, meso-, and metathorax (figs. 1, 2 and 3) are clearly defined in this genus as is usual in this family. Each of these segments has as a basis three primitive ele-

ments, the dorsal plate, or tergum, the ventral plate, or sternum, and the lateral area, or pleuron. The thoracic segments and their elements vary considerably in shape and size. The protergum, or pronotum, is nearly twice as long as the tergum of the metathorax. The mesotergum, still shorter than the latter, is represented by a short triangular area only. The prosternum is about half as long as the metasternum and about one-third the length of the pronotum, giving the pleural area of the prothorax the shape of a trapezium. The mesosternum is present as a plate nearly equal in size to the mesotergum; the mesopleura are also developed in proportion, giving the mesothorax the shape of a short tube. The metathorax, more complicated in structure, represents the segment in which all three primitive elements are well developed and defined.

THE PROTHORAX

In the prothorax the tergal, pleural and sternal areas (fig. 14) are fused, forming a continuous chitinous tube. However, corresponding elements to other thoracic segments are visible due to the different kinds of sculpture. Taxonomically the prothorax bears generic characters but none of specific importance. The two openings of the tube-like prothorax, the anterior and posterior foramina, are bordered by a fringe of closely placed hairs which arise from the inner margin.

Pronotum.—The pronotum (figs. 1, 2, 3 and 14) is one solid plate by which the head is concealed. The dimensions are as follows:

Gn. *materiarius* Fitch., length, 1.23 mm., width, 0.98 mm.
Gn. *retusus* Lec.,   length, 1.44 mm., width, 1.15 mm.
Gn. *sulcatus* Lec,   length, 1.35 mm., width, 1.07 mm.

The measurements are the average of 10 specimens from each species.

Seen from above, the sides of the pronotum are subparallel on the posterior margin, while the anterior margin is broadly rounded. The anterior margin bears 10 to 16 low serrations which are only slightly longer toward the median line and sometimes fused at their base On the anterior area, that is, the area in front of the summit which consists of a short slightly curved ridge and is placed a short distance before the middle of the pronotum, occur many comparatively small and low serrations arranged in concentric rows and decreasing in size towards the summit. Behind the summit the surface of the pronotum is covered with punctures. There are two kinds of punctures; the one comparatively coarse in contrast to the other but fine compared to those in other nearly related genera; the other, minute and only

visible under higher magnification. The coarser punctures are sparse, deep and distinct, the minute ones closely placed giving this part of the pronotum a more opaque appearance. The posterior margin is slightly arcuate. Immediately anterior to the posterior margin there is an impressed line giving the intermediate space the appearance of a low ridge. This raised margin served as one of the main characters in placing this genus near *Pityophthorus* and allied genera. The pronotum is covered with inconspicuous hairs which are longer and
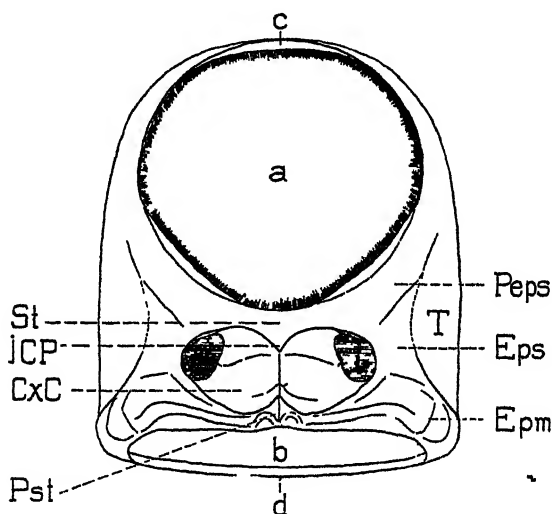
Fig. 14.—*Gnathotrichus sulcatus* Lec.: Prothorax, ventral aspect.

a, anterior foramen; *b*, posterior foramen; *c*, anterior margin of pronotum; *d*, posterior margin of pronotum; *CxC*, coxal cavities; *Epm*, epimeral area; *Eps*, episternal area; *ICP*, intercoxal process; *Peps*, preepisternal area; *Pst*, poststernal area; *St*, sternal area; *T*, tergum or pronotum.

coarser anteriorly. Posterior to the summit occurs a shallow transverse impression. The lateral limitations of the pronotum are not clearly defined but near the postero-lateral angle is a longitudinal ridge which may be considered as a remainder of the pleuro-notal suture.

Pleural area.—The propleural area (fig. 14) is represented as one continuous plate in the shape of a trapezium of which the base is formed by the remainders of the pleuro-notal suture. Ventrally the pleural area is completely fused with the prosternum (St). Externally no sufficiently distinct lines are present to justify the distinction of subdivisional plates as episternum, epimeron, etc. Nevertheless there can be distinguished three parts of different structure which one may call the preepisternal (Peps), the episternal (Eps) and the epimeral

area (Epm). The preepisternal area is flattened, slightly depressed with a surface smooth except for a few minute wrinkles parallel to the longer axis The episternal area is entirely covered by continuations of the serrations which occur on the anterior half of the pronotum. A narrow strip along the posterior margin of the propleuron, quite distinctly limited to the surrounding plates by its transverse wrinkles, may be called the epimeral area.
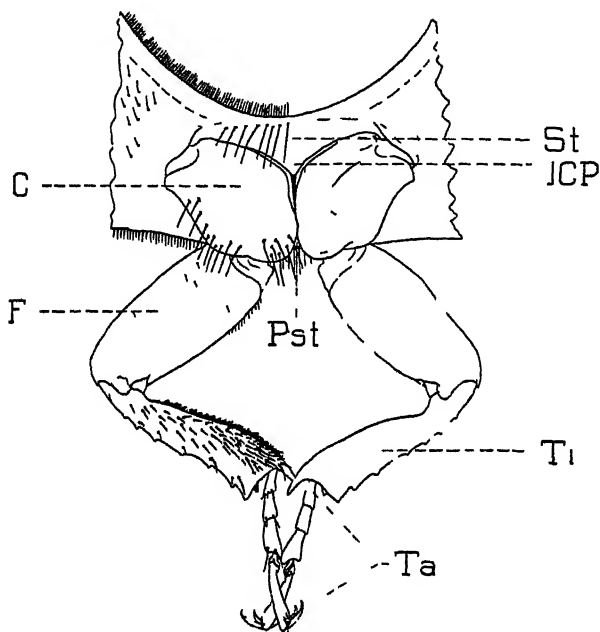
FIG. 15.—*Gnathotrichus retusus* Lec.. Prosternum and fore legs.
C, coxa, *F,* femur; *ICP,* intercostal process; *Pst,* poststernal area, *St,* sternal area, *Ta,* tarsus, *Ts,* tibia

Sternal area.—The lateral ill-defined sternal area is largely occupied by the coxal cavities (CxC). The intercoxal process (ICP) belonging to the intercoxal or sternellar plate is clearly defined and very short so that the coxae touch each other. The sternum proper and the presternal area are again not limited by sutures but by differences in sculpture.

Prothorax—The distinguishing characters of the prothorax are:

1. The pronotum of *Gn. materiarius* Fitch is a little more slender than that of *Gn. retusus* Lec. and *sulcatus* Lec.
2. The punctures of the posterior half of the pronotum of *Gn. retusus* Lec. are somewhat coarser than in the case of the others.

THE MESOTHORAX

The mesothorax is the shortest of the three thoracic segments. The form is that of a ring with the anterior diameter smaller than the posterior one. The meso- and metathorax are very closely connected, giving the appearance of one single unit. Seen from above (dorsal) the scutellum only is visible, while in the lateral and ventral aspect the mesopleura and the mesosterna can be distinguished. The two
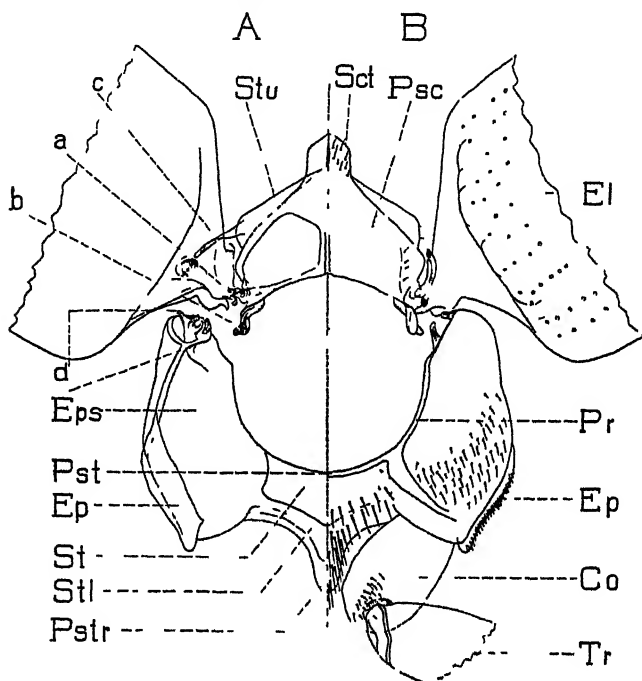
FIG. 16.—*Gnathotrichus retusus* Lec.: Mesothorax, view from anterior foramen. The parts are disconnected by stretching under the coverglass.

A, external aspect, *B*, internal aspect; *Co*, coxa, *El*, elytra; *Ep*, epimeron; *Pr*, preepisternum; *Psc*, prescutum, *Eps*, episternum, *Pst*, presternum; *Pstr*, poststernellum; *Sct*, scutellum, *St*, sternum, *Stl*, sternellum, *Stu*, scutum; *Tr*, trochanter; *a*, articulation of elytra; *b*, clavicola; *c*, pleural hook of scutum, *d*, pleural clavicola.

pairs of appendages are implanted between the pleura and tergum and the pleura and sternum respectively.

Mesonotum.—From the mesonotum or tergum only the scutellum is exposed dorsally. The rest of the notum is covered by the elytra laterally and is hidden by the pronotum anteriorly.

The scutellum.—The scutellum (fig. 16, Sct) is a triangular plate, heavily chitinized, covered with short bristles, and externo-anteriorly fused with the prescutum. There occur slight differences in shape in the different species but they are of no importance.

Scutum.—The scutum (fig. 16, Stu) is represented as two slightly chitinized lobes which are anteriorly fused with the prescutum. The posterior ends are free and lie under the scutellum. A long slender pleural hook (c) originates near the extreme lateral angle.

Prescutum.—The largest area of the mesonotum is occupied by the triangular prescutum (fig. 16, Psc). Externally it forms with the scutellum a smooth continuous plate. The inner side consists of two large and shallow excavations which are surrounded by heavily chitinized ridges. The median ridge is anteriorly divided by two closely placed sutures. Obscure remainders of these sutures are also visible externally and on the scutellum. The extreme anterior corners of the prescutum are produced into two prominent hooks which may correspond to Hopkins' " Lateral arm of prephragma and prescutum " or Korschelt's " Zapenfortsatz des Mesonotums," or Berlese's " clavicola." The clavicola (b) is hinged in parts of the pleural claviculas. At a short distance behind the clavicola is a well developed prealar process which embraces the third axillary of the elytra. On the anterior two-thirds of the prescutum, numerous small punctures are visible externally and near the lateral margin occurs a single row of minute hairs.

The prephragma and the postscutellum are not represented by separate plates. Remainders of the former are probably the wide anterior ridge of the prescutum.

Mesopleura.—The mesopleura are distinctly defined from the tergum and sternum. The largest area of each is occupied by the episternum (Eps) which is a strongly chitinized plate, elongate, with the lateral dorsal area smooth and with a fine pubescence on the lateral ventral area. A narrow strip in front of the episternum, which is defined externally by a suture, and a continuation of it towards the ventral posterior angle of the episternum, may represent the preepisternum. Dorsally the preepisternum is produced into the clavicolardisk. Under the ventral half of the episternum projects a narrow plate, the epimeron (Ep). Preepisternum and epimeron are structureless but the latter bears on its posterior margin a row of fine hairs.

Mesosternum: Presternum.—A narrow ridgelike plate which is fused with the preepisternum (fig. 16, Pr) of the pleura represents the presternum (Pst). The rest of the sternum is externally defined from this by a suture. Internally the suture is obsolate.

Sternum.—The sternum (St) is a rectangular plate with its posterior side produced into an angle, externally fused with the sternellar area or intercoxal process (Stl) but internally defined by a suture. The outer surface is smooth and bears a row of bristles and also a few punctures.

Sternellar area.—The sternellar area is strongly produced posteriorly and internally defined by a suture from the postero-sternellar piece.

Poststernellar area.—This piece (Pstr) is a narrow continuation from the sternellar area. Externally both are covered with long bristles.

THE METATHORAX

Metatergum.—The general appearance and structure is illustrated in figures 1, 2 and 3, which also show the two main parts, namely the notum and the postnotum, or pseudonotum, as the postnotum is often called. The latter is well developed and connected with the notum by a transparent membrane (a). The dorsal aspect of the metatergum is shown in figure 17; the inner in figure 19

Metanotum.—The metanotum (figs. 17, 19) is typical in *Gnathotrichus* in so far as the prescutum (Psc) is only loosely connected with the scutum (Sct). The connection consists medially of a transparent membrane (b); laterally the extreme ends of the posterior prealar process (d) are fused with the lateral margin of the scutular lobes. In this connection it should be mentioned that Hopkins' prescutal lobe seems more likely to be a part of the scutum than of the prescutum. Other modifications are the overlapping of the scutum beyond the posterior prealar process and the development of the scutellum.

The metanotum is clearly defined into three transverse divisions which are the prescutum, the scutum and the scutellum.

Prescutum.—The prescutum (Psc) forms a well developed transverse band extending from pleuron to pleuron. Medially it is bent downwards, forming a ventral reflected lobe which may correspond to the prephragma in other insects. A precosta is not present as a plate defined by lines or sculpture. On the level of the interior origin of the anterior apodeme a suture extends interiorly separating the posterior prealar process from the prescutum proper. This process extends laterally, is covered by the scutular lobe and is fused with it at the extreme end. From the antero-lateral corners of the prescutum proper originate two prominent hooks, the anterior prealar processes (f). Laterally to the anterior prealar process are two disklike formations on each side (g, h) connected with the posterior prealar process. According to Hopkins, the posterior disk (prescutal disk) serves for the small muscles connecting it with the pleural clavicula. A rather intensive investigation would be necessary to determine the purpose of all these formations and homologize them with similar equivalent parts in other groups.
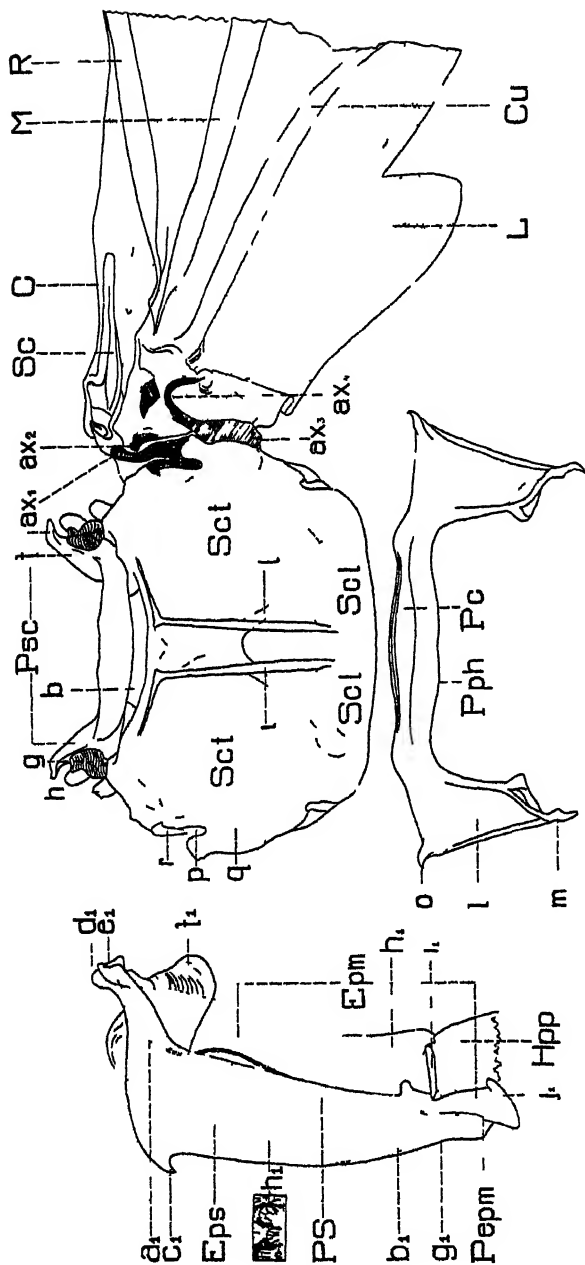
FIG 17—*Gnathotrichus retusus* Lec   Metatergum and metapleuron, dorsal aspect and lateral aspect respectively

C, costal vein, *Cu*, cubital vein, *Epm*, epimeron of metapleuron   *Eps* episternum of metapleuron   *M* median vein   *Pc* precosta of postnotum, *Pepm*, postepimeron of metapleuron, *Pph*, postphragma of postnotum, *PS*, pleural suture   *Psc* prescutum   *R* radial view, *Sc*, subcostal vein, *Scl*, scutellum, *Sct*, scutum, *Hpp*, hypopleurite, *L* posterior wing lobe   *a₁₋₄*, axillaries of the wing base, *b₁*, anterior membrane, *g*, anterior prescutellar disk, *h*, posterior prescutellar disk, *s*, scuto scutellar suture, *s*, median apodeme or endodorsum, *f* anterior prealar process, *l* prealar bridge of postnotum or postscutellum   *m* prealar hook of postnotum, *o*, pleural hook, *p* lateral emargination, *q*, lateral impression, *r* scapular hook, *a₁*, anterior branch of pleural suture, *b₁* posterior branch of pleural suture, *c₁* anterior ventral angle of epistrnum   *d₁* clavicle process, *e₁*, caracoid process   *f₁* pronator disk   *g₁* epimeral suture, *h₁* structure of epistrnum, *i₁* lateral wing lock   *j₁* postepimeral hook

Scutum.—The largest plate of the metanotum is the scutum extending backward from the anterior membrane (b). The limitation between the scutum and the scutellum, the scuto-scutellar suture, is visible as a ventrally elevated ridge which becomes indistinct laterally. The anterior apodeme divides the scutum in two subdivisions, the scutum proper and the scutular lobes. The latter extend beyond the posterior prealar process of the prescutum as was stated above and cover the process dorsally. Externally the scutum is one continuous half spherical plate medially divided by the scutular groove. Internally projections of the scutellum extend far into the scutum. From the inner externo-lateral corners of the scutum proper arise two pairs of parapsidal ridges (k) which converge in a slightly curved line medially.

Scutellum.—The scutellum, which is posteriorly limited by a membrane (a), encloses the scutum in a half circle. The scuto-scutellar suture is produced anteriorly forming the lateral limitations of the scutellar groove. It extends to the anterior margin of the scutum. The space between the produced suture is strongly depressed externally forming a wide scutellar groove. The posterior end of the mesoscutellum rests in this groove. From the posterior lateral corners of the scutellum arise two armlike formations which converge anteriorly meeting at about the middle of the scutum. These formations correspond to the endodorsum (Amans), V-shaped ridge (Snodgrass), or median apodeme (Hopkins). Where they join they are connected with the scutellar groove. It is likely that the intensive study of the endodorsum of the Scolytidae will bring out many new features for the systematic arrangement of this group.

Postnotum.—The postnotum or pseudonotum is subdivided into three transverse divisions, the precosta (Pc), with the prominent prealar bridges (l) and the postphragma (Pph). The precosta is a simple band separated from the postphragma by the postnotal apodeme. Laterally it is produced into prominent prealar bridges. The inner margin is developed as a heavily chitinized ridge which is posteriorly divided, forming a ring and externally produced into a slender hook, the prealar hook (m).

The postphragma is a slightly ventrally bended band. The postnotum is visible externally, giving the appearance of a reduced tergum at the first abdominal segment.

Metapleura.—The pleuron of the metathorax (fig. 17) consists chiefly of two plates, the episternum (fig. 17, Eps) and the epimeron (Epm). The pleural suture (Ps) is externally represented as a distinct line, internally as a ridgelike structure. From the pleural suture

branch three other sutures or ridges. Anteriorly there is a short suture dividing the parapterum from the wing process; posterio-dorsally another ridge separates the postepimeron (Pepm) from the rest of the epimeron. Ventrally another ridge indicates that part of the episternum which is covered by the sternum and the metacoxa.

Episternum.—The episternum is an externally continuous plate having the shape of a narrow triangle with the base facing forward. Ventro-anteriorly it is produced into a hooklike angle, the sternal hook (c_1) or anterior sternal hook of Hopkins. The sternal hook fits into an emargination of the sternum, the clavicula (fig. 18, d). Dorsally the extreme angle of the episternum with the pleural suture (probably also containing elements of the epimeron) is produced into the parapterum (e), or coracoid process, and the wing process, or clavicular process (d). From the underside of the parapterum originates a well-developed pronator, or muscle disk (fig. 17, t_1). The episternum is heavily chitinized and covered by numerous large punctures which are interlaced by a network of fine ridges. See also figure 17, h_1. When the elytra are kept in the closed position the metapleura are nearly completely hidden by them.

Epimeron.—Between the pleural suture and the lateral margin of the metanotum a more flexible, partly membranous sclerite is inserted. Posteriorly it is subdivided by a branch of the pleural suture separating the postepimeron from the epimeron proper. While the epimeron proper is more membranous and flexible, the postepimeron is more heavily chitinized. The postepimeron bears dorso-posteriorly a recurved hook, the postepimeral hook (j_1), which articulates with the clavicula of the sternum of the first abdominal segments. The hypopleurite (Hpp) extends forward up to a shallow emargination on the dorsal margin of the postepimeron. The anterior margin of the hypopleurite is double reflexed, fitting in a reflexed ridge of the inner layer of the elytra. The area between the anterior margin of the hypopleurite and the dorsal nob of the pleural suture is deeply impressed. Epipleurite 1 of the abdomen is situated in front of the hypopleurite closely attached to the scutellum of the postnotum.

Metasternum.—The metasternum is represented as a rectangular continuous plate divided by remainders of a median line. It is illustrated in figure 18. The anterior margin is medially produced into an angle which extends far between the mesocoxae. This angle and the thickened anterior margin may correspond to the presternum of other segments. The anterior lateral angles (a) are modified to receive the sternal hooks of the metaepisternae. Therefore these emarginations should be called the anterior claviculae of the metasternum. Posteriorly the sternum is infolded producing a narrow plate, the

sternellar area   Normally the sternellar area is hidden by the coxae except for the two prolongations between the coxae   These are bent dorsally, giving the support for and articulation of the furca   The
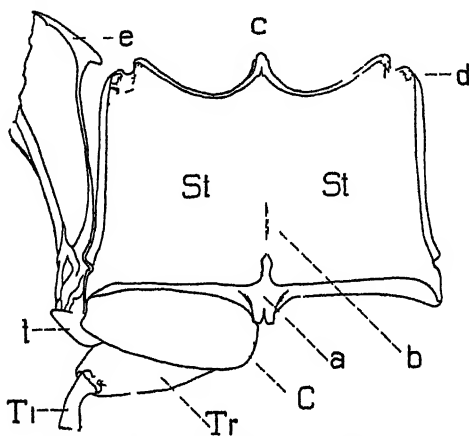
Fig 18—*Gnathotrichus materiarius* Fitch   Metasternum, inner aspect

C coxa, *St* sternum *Ti* tibia, *Tr* trochanter, *a* sternellar area *b* median line, *c*, pre sternellar area *d*, clavicula *e* sternal hook of metapleuron, *t* head of postepimeron
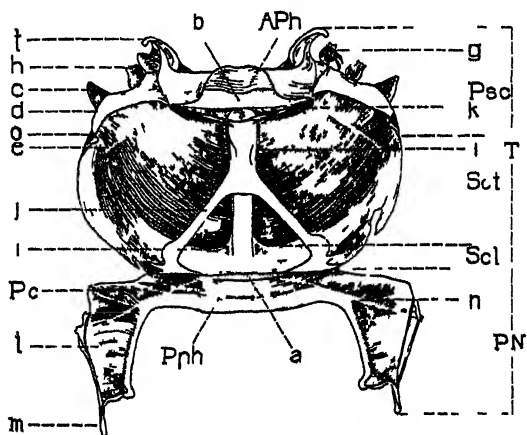
Fig 19—*Gnathotrichus materiarius* Fitch   Metatergum, inner aspect

APh, prephragma *Pc*, precosta of postnotum, *PN*, postnotum, *Pph*, postphragma; *Psc*, prescutum *Sct* scutum *Scl* scutellum *a*, posterior membrane, *b* anterior membrane, *c* scutellar lobe *d* posterior prealar process *e*, anterior apodeme, *f*, anterior picalar process *g*, anterior prescutellar disk *h*, posterior prescutellar disk, *s* scuto scutellar suture, *j*, median apodeme or endodorsum *k* parapsides, *l*, prealar bridge of postnotum, or postscutellum, *m*, prealar hook of postnotum, *n*, postnotal apodeme, *o*, scapular hook

sculpture of the metasternum is minutely rectangulate. The punctures which occur are sparse, the hairs of medium length and more numerous laterally.

The metathorax shows little specific and no sexual modifications.

THE ABDOMEN

The chitinous skeleton of the abdomen shows little specific modification but it bears characters which are of importance in separating the higher groups. The differentiation is mainly in the number of dorsal plates or tergites and the development of the spiculum ventrale in the females. The structure and the relative proportions of the different sclerites are illustrated in figures 1, 2, 3, 20, 21, 22, 23, and 24.

Dorsal plates or tergites.—All the tergites are normally covered by the elytra. In the females seven and in the males eight tergites are well developed. The first six tergites are more or less membranous
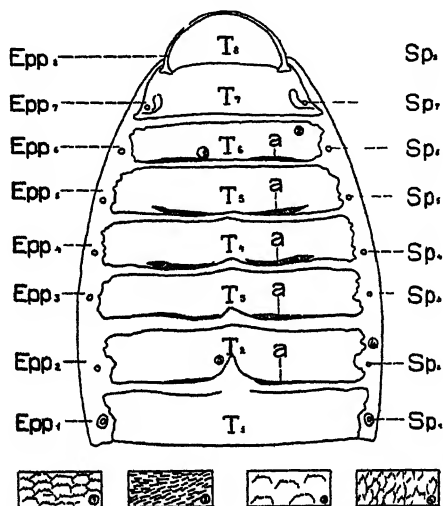
Fig. 20.—*Gnathotrichus materiarius* Fitch, male. Abdominal tergites, ventral aspect.

1, 2, 3, 4, enlarged sections showing details of structure on the dorsal side; *Epp*, epipleurites, *Epp* 7 and 8 fused with tergites, *Sp*, spiracles; *T*, tergites

and flexible in both sexes, yellowish in color, and covered with spinous to toothlike armature on the external surface. The spinelike armature is more medial and posterior on the plates. Near the anterior margin the armature becomes more toothlike, forming broad plates armed with minute spines posteriorly (figs. 20, $T_{1, 2, 3, 4}$). These plates near the median line on the second, third and fourth tergites are stouter and not so densely placed. In the same tergites there is a reduction of the chitinization, forming a membranous emargination. Still another type of armature is found on the pleurites as illustrated in figures 20, 4. The purpose of these armatures is doubtful. The intersegmental membranes are colorless without any markings. Heavily chitinized bands are situated near the posterior margin of plates two

to six. These bands or ridges resemble the parapsides of the meta-
thorax both in structure and in position. Punctures are numerous in
all the plates and the lateral limitations are always irregular. The
seventh and eighth tergites in the males and the seventh in the females
are heavily chitinized and lack the above mentioned armature but
have numerous hairs and punctures.

Lateral plates or pleurites.—The pleural suture seems to be the
line which divides the heavily chitinized hypopleurites from the mem-
branous epipleurites. The pleural suture is not visible in the seventh
and eighth pleurites because the epipleurite is heavily chitinized here
and completely fused with the tergite. The second hypopleurite which
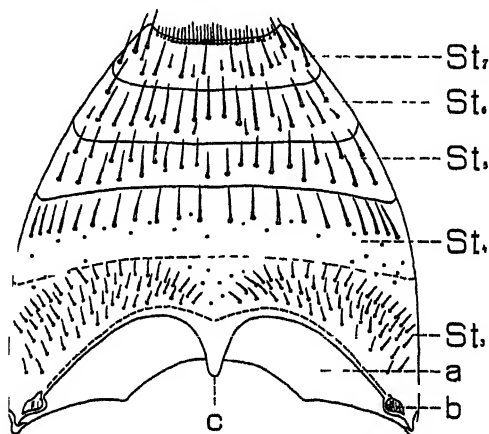
Fig. 21.—*Gnathotrichus materiarius* Fitch: Abdominal sternites, ventral aspect.
St, sternites; *a,* coxal cavity; *b,* clavicula; *c,* intercoxal process.

extends beyond the postepimerum of the metathorax is ventrally de-
fined by a suture while the others are fused ventrally with the sternites.
The former corresponds to the second tergite. The hypopleurite be-
longing to the first tergite is not represented as a plate but fused with
the epipleurite. The hypopleuritic areas are covered by the elytra when
they are kept in the closed position, and form a vertical plane, while the
sternites make an angle of about 120 degrees with them. As was men-
tioned before, the epipleurites are membranous except those which cor-
respond to the last tergites. The hypopleurites corresponding to the
last seventh and eighth tergites are present only as narrow membranes.

Ventral plates or sternites.—In both sexes only five ventral plates
or sternites are distinctly defined by sutures as is illustrated in figure
21 and they represent the sternites three to seven. The sternites are

widest at the base, decreasing in width towards the apex. The first visible sternite is the longest and is separated from the second by a suture which is only visible under high magnification. It is very likely that the first visible sternite contains elements of more than one abdominal segment but they are not indicated by sutures or lines. Medially the first sternite is produced into a long process called the intercoxal process, which extends far between the metacoxae. From
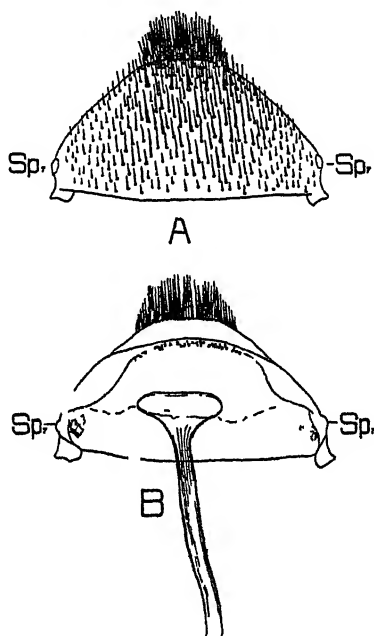
FIG. 22.—*Gnathotrichus retusus* Lec.: Seventh tergite of female.
A, dorsal aspect; *B*, ventral aspect; *Sp*, seventh spiracle.

the base of this process a ridge arises which extends laterally, separating the part of the sternite covered by the metacoxae from the remainder. At the antero-lateral corners this ridge is developed into a clavicula. In this clavicula (b) articulates the ventral part of the postepimeral hook. The surface of the uncovered part of the first sternite bears numerous hairs which are arranged in concentric rows encircling the metacoxae. Punctures are sparse. All the other sternites are separated from each other by deep septae and they have the shape of short rectangular plates of nearly equal length. They are all heavily chitinized and armed with long hairs arranged in a trans-

verse row. The last sternite is infolded on the apex. There occur no striking differences in either different species or in the two sexes.

Spiculum ventrale.—In the females of all three species the spiculum ventrale is well developed. By careful dissection it can be seen fastened to the Fortsatzlappen Verhoeff. Without any doubt we are dealing here with a true spiculum laterale clausum (Fuchs). The median line commissura, which gives by certain modifications the spiculum ventrale opportum, is especially well defined in *Gn. materi-*
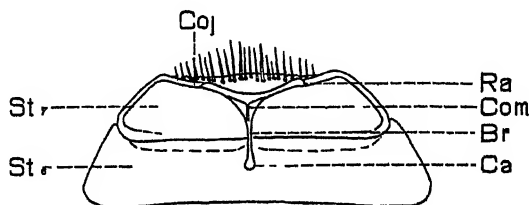
FIG. 23, A.—*Gnathotrichus retusus* Lec.: Sixth and seventh sternites of a female with the spiculum ventrale.

Ca, caput; *Coj*, conjunctus lateralis; *Com*, commissura; *Br*, brachium; *Ra*, radix; *st*, sternites.
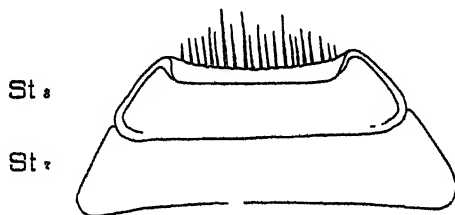
FIG. 23, B.—*Gnathotrichus retusus* Lec.: Seventh and eighth sternites of a male.

arius Fitch and *retusus* Lec. For further studies on this subject it is proposed to name the different parts of the spiculum. The part where the spiculum joins the seitlichen Ansatzlappen (Verhoeff), seitlichen Lappen (Fuchs), may be called radix spiculorum; the more or less chitinized, sometimes membranous bands extending anteriorly, brachium; and the apically thickened part, caput. The seitlichen Lappen (Fuchs), Fortsatzlappen (Verhoeff) should be called the conjunctus lateralis. The spiculum ventralis of *Gn. sulcatus* Lec. may be easily distinguished from the others by its slimmer brachiae. *Gn. retusus* Lec. and *Gn. materiarius* Fitch show no striking differences in this regard.

THE SPIRACLES

Corresponding to the number of the epipleurites, there are eight spiracles in the male and seven in the female. These are implanted in the membranous epipleurites and the apical epipleuro-tergite respectively. The eighth pair of spiracles in the male are always rudimentary. *Gn. materiarius* Fitch shows comparatively the best development in this regard. The seventh epipleurotergite of the female bears a pair of spiracles which are well developed and only very slightly smaller than the others. There also occurs one pair of spiracles on the prothorax. They lie under the produced caudad-lateral angles of the pronotum.
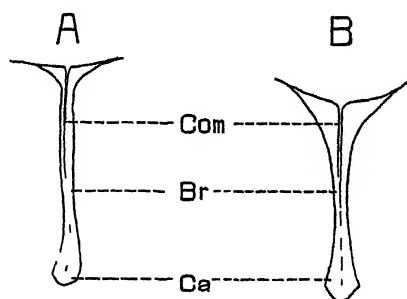
Fig. 24.—Spiculum ventrale in female: A, *Gnathotrichus sulcatus* Lec., B, *Gnathotrichus materiarius* Fitch.
Br, brachium, *Ca*, caput; *Com*, commisura.

THE LEGS

The three pairs of legs are illustrated in figures 25 and 26. They do not vary strikingly from species to species neither in form nor in sculpture. Therefore the drawings were made from *Gnathotrichus materiarius* only. The legs present all the typical segments common in Coleoptera, which are the coxa, the trochantin, the femur, the tibia, the tarsus and the pretarsus.

Coxa.—The coxa (fig. 25) differs considerably in shape in the three pairs of legs. The coxa of the prothorax (A) is very stout, ball-like, the mesocoxa (B) is slightly longer and the metacoxa (C) is nearly twice as long as the forecoxa. The proximal end of the fore- and mesocoxa show distinct indications of a basicostal suture (a). In the fore-coxa the basicostal suture is formed into an external ridge ventrally, which becomes lower and indistinct laterally. In the mesocoxa a simple suture (a) indicates the limitation of the basicosta. The basicostal area of the forecoxa (Bc) is about twice as long as the same structure in the mesocoxa. The basicoxite (Bcx) is present as

a marginal flange and is visible in both the fore- and the mesocoxa. The metacoxa does not show the separation of a basicosta by external lines or internal ridges. The extreme proximal end bears a rather indistinct, internal marginal ridge only.

The three articular surfaces (Snodgrass) are largely modified in the different legs. The pleural articular surface of the fore-coxa is present as the medial, proximal margin of the basicosta only. This part is slightly more heavily chitinized. In the mesocoxa the pleural articular surface (b) is more strongly developed. It consists of a
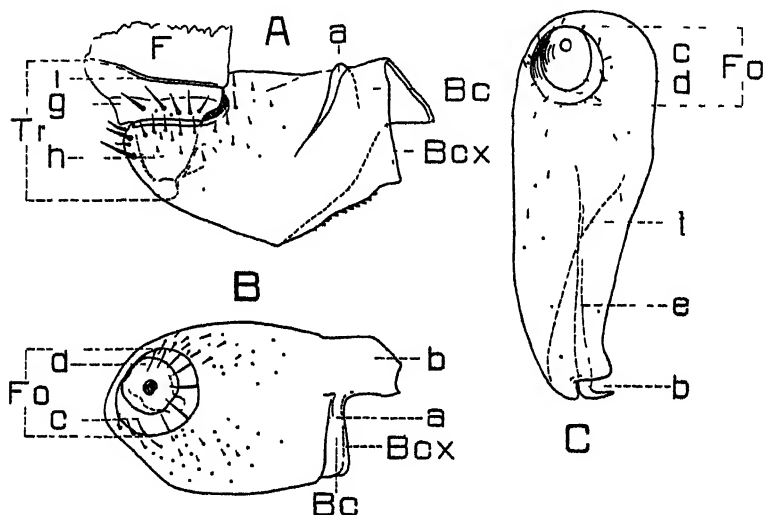
FIG. 25.—*Gnathotrichus materiarius* Fitch: A, forecoxa, lateral aspect; B, mesocoxa, C, metacoxa, both ventral aspect.

Bc, basicosta; *Bcx*, basicoxite; *F*, femur; *Fo*, fossa; *Tr*, trochanter; *a*, basicostal suture; *b*, pleural articular surface; *c*, outer ring of fossa; *d*, inner ring of fossa; *e*, anterior coxal suture; *f*, internal ridge; *g*, basicostal ridge of trochanter; *h*, condyle of trochanter; *t*, trochantero-femoral suture.

projection of the basicosta. In the metacoxa a hooklike structure (b), which is basally fused with the anterior coxal suture, may be considered as the pleural articular surface.

The articulation of the trochantin is monocondylic with the fossa in the coxa. The fossa (Fo) is a circular, conelike, impression on which two main parts are clearly defined; the outer ring (c) with a ridgelike elevation on the external surface of the coxa and the inner ring (d) or bottom which bears a heavily chitinized knob on the inner surface. It is most probable that the outer ring corresponds to the anterior, the inner ring to the posterior or distal articular surface of Snodgrass. Each coxa has opposite to the fossa a circular opening in

the heavily chitinized wall of the coxa which is covered by a thin membrane only. The extreme tip of the trochantinal condyle touches this. Ridges to strengthen the coxal walls do not occur in the fore- and mesocoxa. The metacoxa bears such a ridge on the ventral side
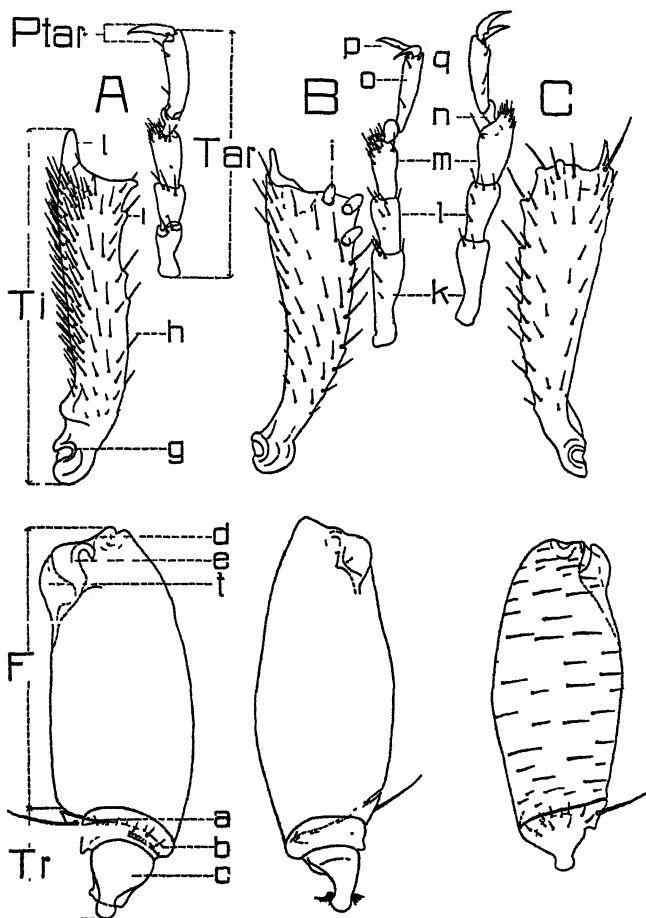
FIG. 26.—*Gnathotrichus materiarius* Fitch: A, fore leg, B, mesothoracic leg, C, metathoracic leg.

F, femur; *Ptar*, pretarsus; *Tar*, tarsus; *Ti*, tibia; *Tr*, trochanter; *a*, trochantero-femoral joint; *b*, basicostal ridge; *c*, condyle of trochanter; *d*, dorsal femoral fossa; *e*, ventral femoral fossa; *f*, anterior groove; *g*, tibial condyle; *h*, outer margin of tibia; *i*, marginal tooth; *j*, apical tooth; *k*, *l*, *m*, *n*, tarsal segments; *o*, apical segment; *q*, arolium; *p*, claw.

which forms a well developed internal ridge (e); this ridge may correspond to the anterior coxal suture (Snodgrass). Another more feebly developed ridge (f) occurs on the dorsal coxal wall.

The hair armature is best explained by the figures. No differences have been found from species to species.

Trochantin.—The trochantin (fig. 26, Tr) is a small structure and is closely attached to the femur. On the ventral or outer side, when the femur is kept close to the body, a deep groove, the trochantero-femoral groove (a) separates the femur from the trochantin. On the dorsal, or inner side, the separation is indicated by a suture only. Structurally, three parts may be distinguished on the trochantin. These are the basicostal ridge (b), the articulatory condyle (c) and the small apical piece (r). The basicostal ridge is a broad, stuffed, ringlike structure which gives the articulation with the coxa an external rest. For the same purpose a hooklike process on the postero-median angle of the basicosta is used. The prominent, cone-shaped articulatory condyle originates basally. The shape of the condyle is alike in all three pairs of legs; the slight differences showing in the plate are due to the different angles from which the drawings were made. The apical piece projects over the basicosta when viewed from above, dorsally, and is fused with the basicosta when seen from below. It bears a long slender spine in all three pairs of legs. The basicosta is externally armed with a few small hairs. From the kind of connection between the femur and the trochantin it can be concluded that but little movement is possible between them.

Femur.—The femur (fig. 26, F) is the strongest segment of the leg and is about equal in length with the tibia (Ti). Basally it is connected with the trochantin; apically, the tibia articulates. The femur is long, oval to rectangular in outline and strongly compressed. The articulation of the tibia is bicondyle (d, e), the femur containing two half circular fossa. There occur no striking differences in the three examined species or in the three pairs of legs in one species. The inner or dorsal surface of the femur is smooth without hairs or bristles; the exposed surface bears numerous rather fine, long hairs which are directed transversely. A deep groove (f) with two lateral winglike extensions occurs latero-apically. This groove allows the tibia to be flexed closely against the femur.

Tibia.—The tibia (fig. 26, Ti) is about as long as the femur, triangular in outline and strongly compressed anteriorly. The proximal end is widened, half circular in outline, and bears the two articulatory condyles. The proximal quarter of the tibia is slightly bent laterally. The dextral margin is without teeth or armations; the sinistral margin bears four to six low serrations and three marginal teeth (i) which are imbedded in sockets. The apical tooth (j) is straight, rather stout and not imbedded in a socket; the subapical tooth is present as a low elevation only. The articulation of the tarsus is membranous.

Tarsus.—The tarsus (fig. 26, Tar) is composed of five joints or segments. They are not articulated by hinges with each other but they are movable by means of inflected connecting membranes. The first three segments (k, l, m) are subequal in length and shape. The basal segment or basitarsus does not show any special armations such as occur in other genera. The fourth segment (n), the smallest of the tarsus, resembles somewhat in shape the trochantin. This segment which is often highly modified in the *Scolytidae,* is short and knoblike in *Gnathotrichus.* The apical segment (o) is longer than segments one to three, more slender and slightly curved. Except the fourth, all tarsal segments bear at least a few hairs scattered over the entire length. The third segment also bears a plushlike arrangement of hairs apically.

Pretarsus: the terminal segment.—The terminal foot structure (fig. 26, Ptar), which has been called praetarsus, Krallenglied, unguis, ungula and pretarsus by different authors, bears two simple claws (p). The areolium (q) is membranous and heartshaped.

THE WINGS

As in all the *Scolytidae, Gnathotrichus* Eichh. has well developed elytra or mesothoracic wings and hind or metathoracic wings. The development of the metathoracic wings would indicate, as has been found to be the case, that the species of this genus are good fliers. No attempt will be made in what follows to speculate on the functions of the different sclerites of the articulation of the wings since the author has had no opportunity to make observations on them. Merely a description of the different parts will be given which it is hoped may be of value for future taxonomic and physiological studies.

MESOTHORACIC WINGS OR ELYTRA

The mesothoracic wings consist as usual of two layers of integument, both of which are chitinized, the outer layer however being much thicker than the inner layer. The space between these two layers contains the tracheal and circulatory systems. The punctures which mark these wings externally indicate, according to Hopkins, the points of union between the two layers. The form and general structure are shown in figures 1, 3, 16 and 27. The elytra when closed and viewed from above are as wide as or slightly narrower than the pronotum, with the sides subparallel, slightly tapering toward the apex and broadly rounded behind, the extreme external margin subacute.

Basal area—The basal area (fig. 29), as here interpreted, is the basal part of the elytra itself and the sclerites which form the connection with mesonotum and the mesopleura respectively. The articulatory elements of the elytra itself are made up chiefly of the projected costa (Co) and subcostal veins (Sco) and the costal (a) and the subcostal heads (b). These heads articulate with the mesopleural clavicola (fig. 16, d). There are also four distinct axillaries (fig. 29, ax_1 to ax_4) or pteraliae. The first axillary (ax_1) partly encloses
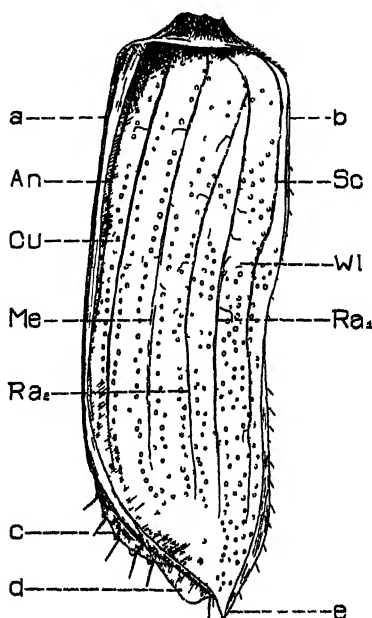
FIG. 27.—*Gnathotrichus retusus* Lec.: Left elytron, ventral aspect.

An, anal; *Cu*, cubitus; *Me*, media; *Ra*, radius; *Sc*, subcosta; *Wl*, lateral wing lock; *a*, dorsal or sutural margin; *b*, costal margin; *c*, lateral convexity; *d*, stridulating scraper; *e*, apex.

the tegula and fuses at its apex with the second axillary. The second axillary (ax_2) articulates at its base with the prealar process (a) of the prescutum. The apex of the second axillary forms a heavily chitinized clamp in which the elytra fits as a tongue. The third axillary (ax_3) corresponds to Hopkins' flexor plate. It commences on the internal surface of the second axillary and ends on the external surface of the elytra. It is believed that a sclerite (ax_4) projecting from the posterior margin of the tegula is the fourth axillary. The tegula (Te) is well developed, having the form of a hairy pad.

Tracheation.—All six primary veins (fig. 27) are present and these run roughly parallel and equidistant from each other the whole length of the wing. The costal vein is fused with the corrugated and thickened anterior margin (b) forming an anterior ligature of the wing. The subcostal (Sc), medial (Me), cubital (Cu) and anal veins (An) are simple; the radius is split into two branches (Ra$_1$, Ra$_2$). The finer divisions of the tracheae permeate the spaces between the veins producing a fine network. Between the adjacent veins there are situated two fairly well defined rows of punctures.

Sculpture and vestiture.—The occurring punctures are as previously mentioned arranged in approximate rows, being more confused
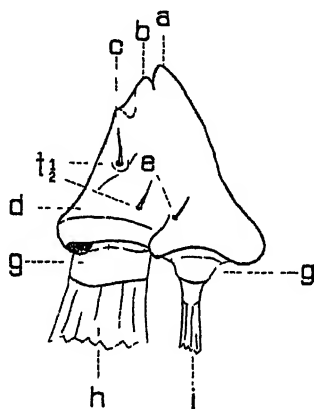
FIG. 28.—*Gnathotrichus materiarius* Fitch: Mandibles of the larva.

a, apical tooth; *b,* subapical tooth; *c,* median tooth; *d,* molar tooth; *e,* lateral bristle, or seta (seta mandibulae lateralis); *f$_{1-2}$,* dorsal setae, or bristles (seta mandibulae lateralis); *g,* retractor tendon; *g$_1$,* extensor tendon; *h,* retractor disk; *i,* extensor disk.

laterally and on the declivity. The interspaces are minutely recticu-late and punctulate and in all three species about alike. From the punctures originate minute hairs which are slightly longer on the declivity. There also occur longer bristles but they are scarce and scattered over the entire surface, being more numerous on the declivity.

Lateral wing lock.—On the inner lateral side of the elytra at the level of the anterior margin of the hypopleura a short transverse ridge (fig. 27, Wl) is situated. That ridge is recurved, fitting into a similar formation which is formed by the anterior margin of the hypopleura (fig. 1, f, fig. 17, i$_1$). These two parts interlock and are apparently intended to keep the elytra closed.

Declivity.—The extreme lateral margin of the elytra is subacute. The declivity itself is sloping with a more or less distinct sulcus on

each side of the median suture. The lateral convexities (fig. 27, c) bear at least faint traces of granules from which bristles arise. There also occur a few bristles near the apex of the declivity.

Stridulating accessories.—In both sexes the left elytron bears on the declivity a well developed lobe which lies under the right elytron
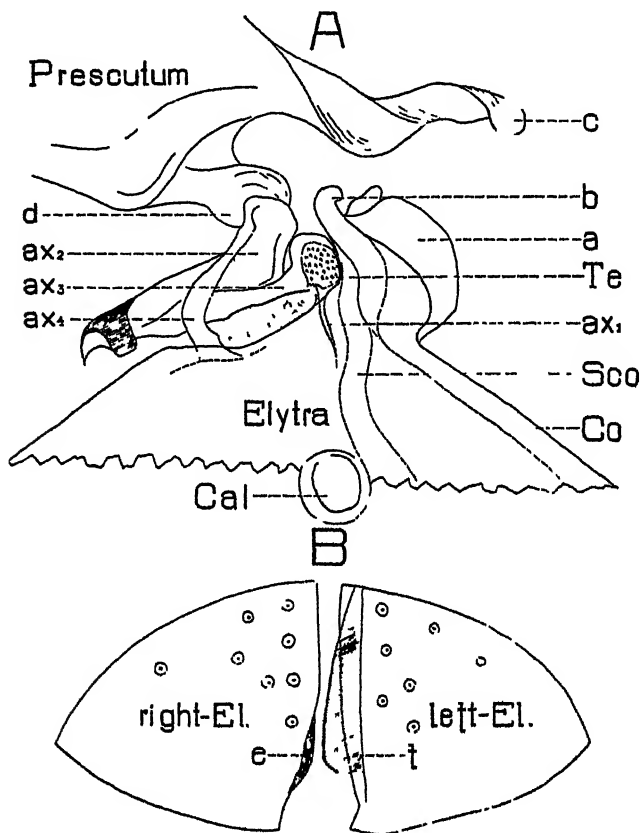
Fig. 29.—*Gnathotrichus retusus* Lec.: A, articulation of the elytra, ventral aspect; B, stridulating apparatus on the apex of the elytra, ventral aspect.

Cal, callus; *Co,* costal ridge; *Sco,* subcostal vein; *Te,* tegula; *a,* costal head; *b,* subcostal head, *ax₁, ax₂, ax₃, ax₄,* the axillaries; *c,* lateral arm of prephragma Hopk., or pleural hook of scutum; *d,* prealar process; *e,* stridulating rasp; *f,* stridulating scraper.

when the elytra are kept in the closed position. This lobe, the stridulatory scraper (fig. 27 d, fig. 29 f) is finely transversely sulcate on the dorsal side. The corresponding area on the right elytron (fig. 29, c) is also rasplike but only on a narrow strip. If these two parts are grated against each other, it is most probable that they will produce a chirping sound. Up to date this sound has not been heard by the

author and therefore this statement is merely an attempt to explain these two parts of the elytra.

Specific modifications of the elytra.—While *Gnathotrichus* shows the strongest development of the declival sulci, with lateral convexities and granules on the latter, these characters decrease in development in *Gn. sulcatus* Lec. and are faint in *Gn. materiarius* Fitch. There also occur many variations from specimen to specimen so a determination cannot be based on these characters only.

METATHORACIC WINGS OR HIND WINGS

The metathoracic wings (figs. 3, 17) are homologous with the meso-thoracic wings but differ considerably in structure and development due to their use as flying apparatus. In the genus *Gnathotrichus* Eichh. no specific modifications of importance have been observed.

As in all genera of this family the wings are folded together and covered by the elytra when the beetles are at rest. The hind wings are twice as long as the elytra and three times as long as wide. Near the base on the inner side occurs a deep emargination separating a distinct lobe from the wing—the posterior wing lobe (fig. 3, WL, 17, L). The shape of the wings is very much alike in all three species, long oval with the anterior and posterior margins nearly parallel.

The wings consist of two layers of integument enclosing the tracheal system. In the hind wings both of these layers are membranous except on the veins and the basal sclerites. Externally they are covered with microscopic hairs, except on the basal heavy parts of the veins and the axillaries (fig. 17).

Veins.—The venation of the wings shows considerable reduction. The only visible veins are the costa (fig. 3, Co), subcosta (Sco), radius $(R_1 + R_2)$, media (M_1, M_2) and cubitus (Cu_1). The radial and the medial veins are split into two branches.

Costa.—As Hopkins has shown for the genus *Dendroctonus,* the costal vein (fig. 3, Co, 17, C) is also in *Gnathotrichus* Eichh. confined to a short basal piece. Apically it does not join another vein but is reduced so that the costal margin is occupied by a membrane only up to the point where the radial vein is bent forward and structurally replaces the costa. The base of the costa is produced into the so-called costal head (fig. 30, CoH). It consists of two parts, the costal condyle (fig. 30, a), and the costal pocket (b). The former articulates with the clavicle process of the metaepisternum (fig. 17, d_1). From the base of the costal condyle a pocket stretches to the subcosta. At about the center of the pocket a projection of the subcostal head, the sub-

costal hinge (fig. 30, c), is attached by tendons giving the motion of a hinge joint. This attachment enables the subcostal head to move in the pocket.

Subcosta.—The subcosta (figs. 3, Sco, 17, Sc, 30, Sco) consists of a chitinous band extending apically as far as the costa and strengthened by two ridges of dense chitin. The basal part, or subcostal head (fig. 30, ScoH), as it was called by Hopkins, is anteriorly formed into a
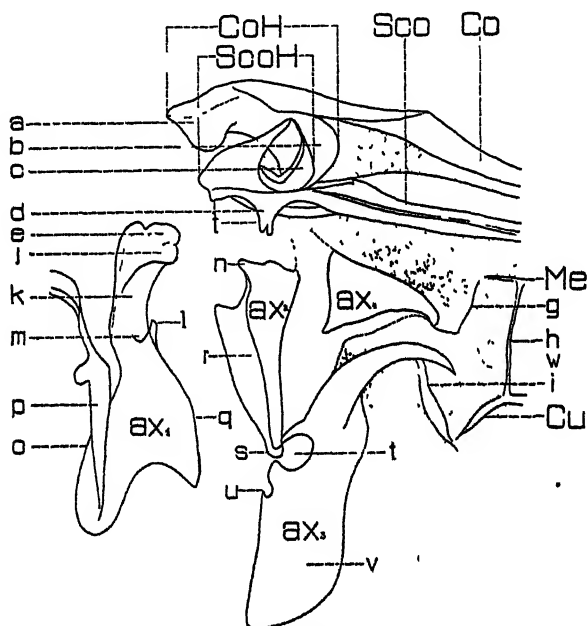
FIG. 30.—*Gnathotrichus retusus* Lec.: Basal area of the wing, wing articulation.

Co, costal vein; *Coll,* costal head; *Cu,* cubital vein; *Me,* medial vein; *Sco,* subcostal vein; *ScoH,* subcostal head; *a.x,* axillary plates; *a,* costal condyle; *b,* costal pocket; *c,* subcostal hinge; *d,* subcostal labrum, *e,* condyle of first axillary; *f,* subcostal fossa; *g,* membranous fold connecting *Me* and *a.x₁; h,* membranous fold connecting *Me* and *Cu; i,* membranous fold connecting *Cu* and *a.x₃; j,* epicondyle of *a.x₁; h,* scapula arm; *l,* axillary horn; *m,* axilla; *n,* anterior process of *a.r₂; o,* articulatory margin; *p,* scapular hook of prescutum; *q,* apical margin; *r,* lateral groove; *s,* axillary tendon; *t, u,* lateral emarginations; *v,* posterior part, or handle; *w,* anterior part, or blade.

projection which is composed of a circular band of chitin (fig. 30, c), articulating with the costal pocket. The posterior part forms a fossa, the subcostal fossa (f), which articulates with the condyle (e) of the first axillary. The labrum (d) of the fossa is deeper on the outer side than on the inner. The outer side of the labrum is divided at its free edge by a V shaped groove.

Radius.—The radius (figs. 3, R, R₁, R₂, 17 R) is not directly fused with any of the axillary plates but is basally closely connected with the subcosta. From the point of fusion with the subcosta the radius

extends to the folding hinge on the wing gradually increasing in width. The anterior border of the radius becomes the anterior border of the wing just after the reduction of the costa and subcosta. The folding hinge occurs as a V-shaped plate, the point of the V being anterior. From the folding hinge the radius is divided into two branches (R_1 and R_2). Radius 1 extends as a broad chitinous band along the anterior border of the wing to its apex gradually diminishing in width. Radius 2 is slightly narrower than R_1, running two-thirds with, and parallel to it.

Media.—The media (figs. 3, M, 17, M and 30, Me) is connected to axillary four (fig. 30, ax_4) by a membranous fold (g) of L shape. Another fold (h) runs posteriorly to the cubitus (Cu). From the base to the level of the folding hinge it is continued as a single vein. At the latter point it is divided into two branches (fig. 3, M_1 and M_2), both of which extend to the anal margin. The connection between the single basal part of the media and M_1 is membranous, while M_2 is a direct continuation of the former.

Cubitus.—The cubitus (figs. 3, Cu, 17, Cu and 30, Cu) is connected with axillary three (fig. 30, ax_3) by a membranous fold (i) which runs from the base of the cubitus anteriorly. From its base the cubitus proceeds toward the anal margin which it does not reach. No other branches of the cubitus nor an anal vein are present.

Wing articulation.—The articulation of the wings (figs. 3, 17 and 30) is brought about by means of the costal and subcostal heads, the axillaries of the wings, the clavicle and coracoid process of the metaepisternum, the scapular hook of the posterior prealar process of the prescutum and a series of muscles and tendons connecting and moving these parts. The connection of the costa and subcosta to each other and the costa with the metapleuron was discussed before. In the following lines the axillaries and their connection with the metatergum and metapleuron will be explained.

The axillaries are chitinous plates, differing in number in the different orders and also it seems in the genera of the Scolytoidea, which function as articulatory accessories. In the genus *Gnathotrichus* Eichh. four of such plates are distinctly developed. The heads of the costal and subcostal veins are here not counted as axillaries because they are fused with the veins in such a way that separations seem unnecessary.

First axillary.—The first axillary (fig. 30, ax_1) or scapular plate, as it was called by Hopkins, is very similar in shape to that of *Dendroctonus valens* Lec. as it was illustrated by Hopkins. Anteriorly it is produced to a condyle (e) with a distinct epicondyle (j), articulat-

ing with the fossae (d) of the subcosta. The slender part posterior to the condyle, which was called the scapular arm by Hopkins (k), bears a hornlike process (l), the axillary horn. The horn forms with the scapular arm an axilla (m) in which the anterior process (n) of the second axillary rests. The margin towards the notum or articulatory margin (Hopkins) (o) is connected with the posterior prealar process of the prescutum by the scapular hook (p) and tendons. The scapular hook is a heavily chitinized hooklike plate on the lateral margin of the prealar process. The margin towards the apex (q) of the wing fits into the lateral groove (r) of the second axillary. The base of the scapular plate is deeply emarginated.

Second axillary.—The second axillary (fig. 30, ax_2) or subscapular plate has the shape of an equilateral triangle with its base anteriorly. The side towards the first axillary bears a deep groove, the lateral groove (r), which encloses the apical margin of the first axillary (q). With axillary four it is connected by a membrane only while a well developed tendon (s) connects axillaries two and three on its posterior end. By means of this tendon a strong connection is brought about from the posterior prealar process to the first, second and third axillaries.

Third axillary.—The third axillary (fig. 30, ax_4) or flexor plate (Hopkins) has the shape of a sickle with two emarginations (t, u) on its inner side. The anterior one (t) ends in the tendon connecting axillaries two and three. The handle of the sicklelike plate (v) is without special characters. The blade (w) shows on its posterior margin near the apex a membranous fold (i) connecting this plate with the cubital vein.

Fourth axillary.—The median plate (Hopkins) corresponds to the fourth axillary (fig. 30, ax_4). It is triangular in shape, connected to the median vein by a membranous fold (g) and to the other axillaries by membranes only.

When the radial plate (Hopkins) is not considered as a distinct plate but as a connecting tendon between the second axillary and the radial vein only, the shape and structure of the other axillaries are very much alike in the widely separated genera *Dendroctonus* Er. and *Gnathotrichus* Eichh. Further studies will show if this means a parallel modification or if we have to deal with a character common to the superfamily of the *Scolytoidea*.

Lateral impression.—An area distinctly impressed on the metascutum (fig. 17, q), according to Hopkins, accommodates the flexor plate at rest when the wings are closed.

Lateral emargination.—The lateral emargination (Hopkins) (fig. 17, p) is an emargination on the scutum on the lateral margin of the scutellar lobe in which is implanted the inner posterior lobe of the scapular plate and the scapular hook. The latter connects the posterior prealar process with the scapular plate and the scutellar lobe, respectively.

THE MALE REPRODUCTIVE ORGANS

The male reproductive organs consist, as shown by Nuesslin for this family, of elements of endodermal and of ectodermal origin. These two groups of elements are separated in the larvae and become connected during the pupal stage. Of endodermal origin are the testi (fig. 31, Te), the vasa deferentia (fig. 31, Vd) and the
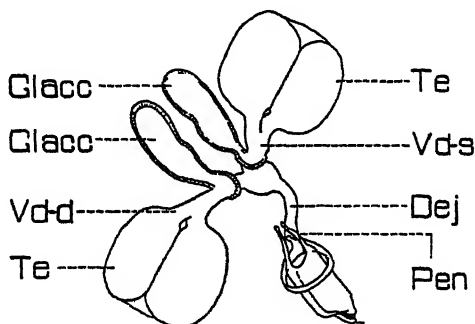
FIG. 31.—*Gnathotrichus materiarius* Fitch: Male reproductive organs.
Dej, ductus ejaculatorius; *Gl. acc,* accessory glands; *Pen,* penis; *Te,* testi; *Vd-d,* vasa deferentia, duplex; *Vd-s,* vasa deferentia, simplex.

mesadenic, or mucous glands (fig. 31, Gl. acc). On the other hand, the seminal vesicle (in part, fig. 33, Rec.), the ductus ejaculatorius (fig. 31, Dej) and the penis (fig. 3, Pen) are of ectodermal origin. The point of connection of these elements is plainly visible in the adults. The distal part of the vasa deferentia and the mucous glands join a short, usually narrow tube, " Zunge " (Nuesslin) ; the latter connects with the ductus ejaculatorius. Externally the Zunge, an endodermal structure, is encircled by a wider tubelike or sphericle envelope, which consists of two parts, the distal end or " Mantel " (Nuesslin) of endodermal, and the basal part or " Becher " (Nuesslin) of ectodermal origin. These last mentioned structures are seen commonly as a ball-like widening of the ductus ejaculatorius and are usually called the seminal vesicle.

The following description is based on *Gnathotrichus materiarius* Fitch only.

The testes consist of two oval structures which are closely connected medially. The vasa deferentia is Y shaped. The mucous glands are wide and stout and about as long as the testi. The seminal vesicle is represented by a subsphericle structure to the upper side of which the glands are joined. The ductus ejaculatorius is comparatively short, stout, and as long as the testi. In Nuesslin's key to the larger groups of Scolytidae, based on the male reproductive organs except the penis, *Gnathotrichus* falls near to the *Ernoporinae*.

Penis.—In order to consider the penis of *Gnathotrichus*, it is first necessary to discuss in a general way the *Scolytid* penis.

Lindeman, who was the first investigator of the *Scolytid* penis, distinguished two main groups of elements, the primary and the accessory. He states that the primary elements, which comprise the body (Koerper), the fork (Gabel) and the stalk (Stengel), are constant throughout the family *Scolytidae*, while the accessory elements, which form together the so-called Aufsatz, vary considerably in the different genera as well as from species to species in one genus. Verhoeff, the second to deal with the subject, did not agree with this classification, while Nuesslin supported Lindeman's opinion. The last of the more important investigators of the *Scolytid* penis, Dr. Fuchs, constructed a new system for such a classification, without consideration of the phylogeny, and distinguished covers (Huellen), inclosed parts and parts external to the covers. The author cannot agree with Lindeman and Nuesslin that the primary elements always included in the Scolytid penis consist of the fork (parameren Verhoeff) and the stalk (spiculum ventrale (Fuchs)). Already Fuchs has shown how far the reduction of the parameren and the spiculum ventrale in the European *Hylesinidae* has gone and the author is convinced that more intensive investigations of this subject will bring up many new facts. Without doubt more than three-quarters of the genera and ninety per cent of the species of the *Scolytidae* have not been studied at all or not thoroughly enough. For example, it was found in the present study that the spiculum ventrale is absent in *Gnathotrichus,* and it will not be long until genera are found in which the complete loss of the parameren occurs. If it is desirable to distinguish between primary and accessory elements, the author would prefer that the primary elements be considered the body only, the accessory elements all the parts outside of it. For further studies of this subject, the author will adopt Dr. Fuchs' classification and nomenclature until a time when sufficient new material is available to furnish new conclusions.

The penis presents, in the genus *Gnathotrichus,* excellent generic as well as specific characters The following discussion is based on slides which were made from dried material treated with 10% sodium-hydroxide solution Dr Fuchs distinguished two layers of covers, the outer and the inner. These two layers were also found to be present in *Gnathotrichus* The outer layer consists of a membranous tube
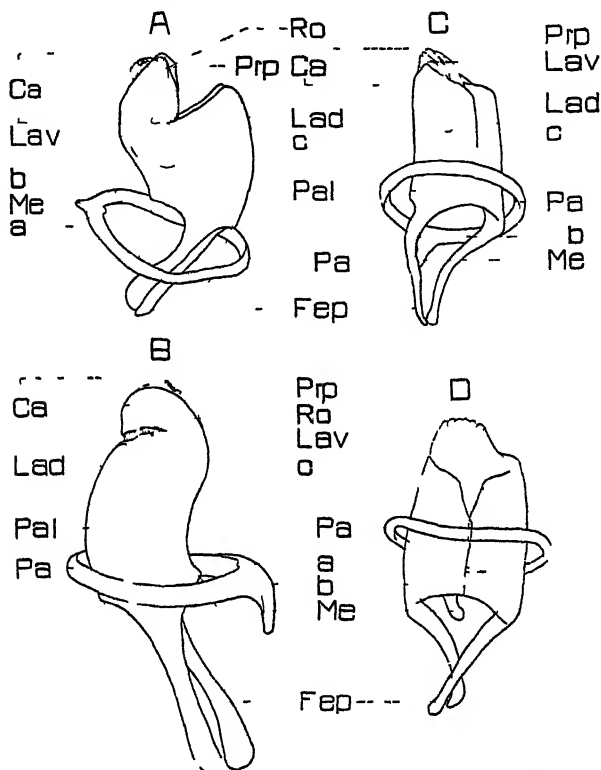
FIG. 32—A, *Gnathotrichus sulcatus* Lec , B, *Gnathotrichus retusus* Lec , C, D, *Gnathotrichus materiarius* Fitch · A, B, C, lateral aspect, D, dorsal aspect

Ca, caput, *Fcp* femora penis, *Lad,* laminae dorsales, *Lav,* laminae ventrales, *Me* metula, *Pal,* pallidium, *Pa,* pirameren, *Prp,* preputial sac, *Ro,* rostrum, *a,* ventral nob of the parameren, *b,* tegmen furcae, *c,* internal ridge on *Lad*

in which the inner cover slides forward and backward. A ringlike part of this tube is heavily chitinized, and when dried specimens are used only this structure is obtained It was called by Lindeman the gabel, the parameren by Verhoeff and the tegmen by Hopkins. The inner cover consists of a second tube which is heavily chitinized throughout and which shows remarkable variations from species to species Figure 32 illustrates the peni of the genus under examination.

Parameren.—In *Gnathotrichus* the parameren (Pa) is a heavily chitinized ringlike structure. It is entire, without a dorsal transverse suture or knoblike projection cephalad, as in *Pityogenes* Bedel, and was called umbellicus by Fuchs. Ventrally, a faint suture is visible in *Gn. sulcatus* Lec. and *retusus* Lec. only. A prominent, heavily chitinized hook extends cephalad from the ventral suture. This structure was called the metula (Me) by Fuchs and the apodemal process by Hopkins. In *Gn. retusus* Lec. and *sulcatus* Lec. a second, caudad, but much smaller knob (a) is present. The tegmen furcae (Fuchs) (b), which are a lateral continuation of the metula, are weakly developed. Lateral widenings of the parameren, Seitenfluegel (Fuchs), are absent.

Specific modifications:—

A—Parameren without small knob ventro-caudad; metula long but slender. *Gn. materiarius* Fitch.

AA—Parameren with small knob ventro-caudad; metula variously modified.

    B—Metula short, weakly developed. *Gn. retusus* Lec.

    BB—Metula long, strongly developed. *Gn. sulcatus* Lec.

Inner covers.—The inner cover (Fuchs), the body (Hopkins), the penis tube (Nuesslin) is a tubelike structure, bilateral-symmetric. On the inner covers three main parts may be distinguished which are the lamina dorsales (Lad), the laminae ventrales (Lav) and the peduculi penis (Fep). The dorso-caudad portion of the inner covers was called the Endplatten by Lindeman, the laminae dorsales by Fuchs and the dorsal plates by Hopkins. The laminae ventrales (Fuchs) or ventral plates (Hopkins) are the corresponding ventral portion of the laminae dorsales. In the genera *Pityogenes* Bedel, *Ips* de Geer, *Pityokteines* Fuchs, *Neothomicus* Fuchs, and others, the laminae dorsales and ventrales are largely separated by deep emarginations caudad giving the laminae the shape of four free projections which are connected basally only. The basal, fused, entire part of the laminae ventrales is the pallidium (Fuchs (Pal)). The sometimes narrow band connecting the two dorsal plates is the jugum or Steg (Fuchs). In *Gnathotrichus* the laminae dorsales and ventrales are fused laterally. Dorsally, the two laminae dorsales are separated by an obscure suture only. The laminae ventrales are fused ventrally, open on the extreme caudad portion. The laminae dorsales as well as the laminae ventrales bear numerous sensory pores on the caudad half. The latter is strengthened by a stronger chitinized band, the caudad limitation of which (c) is strongly emarginate. This chitinous strengthening was called the

radius by Fuchs and this is well developed in all three species of *Gnathotrichus*. A corresponding strengthening on the laminae dorsales, which as the manubrium (Fuchs) is well developed in the genus *Pityogenes* is obscure in *Gnathotrichus*. The caudad portion of the laminae ventrales, the caput (Fuchs), is variously modified, sometimes bearing a beaklike projection dorsally which was called the rostrum by Fuchs. The caput and rostrum vary considerably in shape and development in the genus *Gnathotrichus*. The area of the pallidium, from which the peduculi penis originate, the radix (Fuchs), is not characterized by a heavier chitinization. The peduculi penis were also called Fuesschen by Lindeman, femora penis by Verhoeff and body apodemes by Hopkins. In the normal position the peduculi penis are parallel; when mounted on slides they usually cross each other. Cephalad the peduculi are slightly widened, their connection with the pallidium is solid, not hingelike.

Enclosed parts.—The enclosed parts are a short part of the ductus ejaculatorius, the preputial sac and chitinous strengthenings of the latter. The ductus ejaculatorius is easily recognized by its enclosing muscle structure. The author was able to trace this structure as far caudad as the radius (c) extends. The preputial sac (Prp) consists of a colorless membrane without any chitinous strengthenings. It seems to be connected with the ductus ejaculatorius at the anterior emargination of the radius. Chitinous structures such as the Rinne (Fuchs) do not occur in the genus *Gnathotrichus*.

Parts outside of the covers.—It was stated in the introduction to the discussion of the penis that no indications of the spiculum ventrale are present in the genus *Gnathotrichus*. While in *Xyloterus* Er. and in some genera of the European *Hylesinidae*, the reduction of the Rinne (Fuchs) mostly is followed by a stronger development of the spiculum ventrale, *Gnathotrichus* presents a complete reduction of both.

Generic characters of the penis.—Spiculum ventrale absent; parameren an entire ring, metula well developed; laminae dorsales and ventrales fused laterally, the laminae dorsales dorsally separated by an obscure suture, the laminae ventrales fused except on the extreme caudad portion, the laminae forming a tube, radius distinct, manubrium obscure, jugum and pallidium not clearly defined; sensory pores on the caudad half of the laminae dorsally as well as on the laminae ventrales; the latter always extending farther caudad than the former; the peduculi penis slender, slightly widened cephalad, about as long as the laminae dorsales, connection with the pallidium solid not hingelike; Rinne absent, preputial sac about as long as half of the laminae ventrales.

In the classification of the *Scolytidae,* based on the chitinous skeleton of the penis by Nuesslin, *Gnathotrichus* would have been in contrast to all the other genera. This is easily explained by the fact that only this one character was used in placing the genera. The author has no reason to believe that *Gnathotrichus* is not a highly specialized genus of the *Pityophthorinae.*

Specific modifications:—

A—Parameren without ventro-caudad knob, metula long but slender; laminae dorsales with their dorsal margin straight, the dorso-caudad angle obtuse and broadly rounded, the posterior margin is directed ventro-caudad from this angle; the laminae ventrales with their ventral margin straight, only slightly projecting caudad farther than the laminae dorsales, caput weakly developed, nearly in line with the dorso-caudad margin of the laminae dorsales, rostrum obsolate; peduculi penis about as long as the laminae ventrales, very slender, only very slightly widened at the cephalad end, basal part narrow. *Gn. materiarius* Fitch.

AA—Parameren with ventro-caudad knob opposite the metula, the latter variously modified; laminae dorsales with the dorsal margin broadly arcuate, the dorso-caudad angle variously modified either slightly acute but rather broadly rounded or almost evenly arcuate with the dorsal margin of the laminae dorsales; the laminae ventrales with their ventral margin distinctly incurved, much farther projecting caudad than the laminae dorsales, caput strongly developed, rostrum distinct; peduculi penes vary in length, stouter, more strongly widened at the cephalad end, basal part distinctly widened.

B—Metula short, weakly developed; the dorso-caudad angle slightly acute but rather broadly rounded, the posterior margin is directed ventro-cephalad from this angle, caput not evenly rounded caudad, more tube-like, ventro-caudad margin oblique, the dorsal angle of the rostrum extending to about half of the width of the combined laminae dorsales and ventrales, between the cephalad margin of the rostrum and the caudad margin of the laminae dorsales, a wide, rectangular space membranous; peduculi penis as long as the laminae dorsales on the dorsal margin. *Gn. retusus* Lec.

BB—Metula long, strongly developed; the lamina dorsales with their posterior and caudad margin almost evenly rounded throughout; caput evenly rounded caudad, half sphericle, the membranous space between the cephalad margin of the rostrum and the caudad margin of the laminae dorsales narrow, slitlike, the dorso-cephalad angle of the rostrum and the dorso-caudad angle of the laminae dorsales in one level; peduculi penis distinctly longer than the laminae dorsales. *Gn. sulcatus* Lec.

THE FEMALE REPRODUCTIVE ORGANS

The female reproductive organs (fig. 33) were examined from *Gn. materiarius* Fitch only. As in all Rhychophora, two pairs of
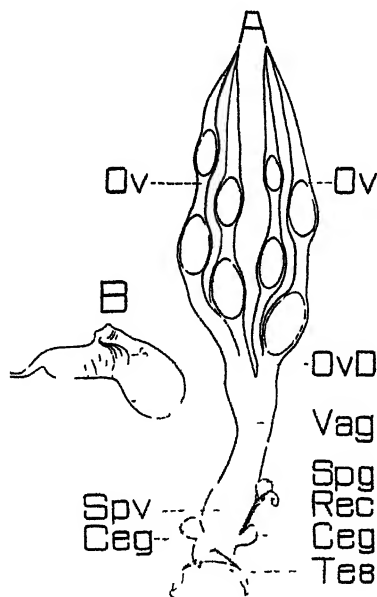
FIG. 33.—*Gnathotrichus materiarius* Fitch.: Female reproductive organs. *A*, the complete organs; *B*, receptaculum seminis; *Ceg*, cement glands; *Ov*, ovaries; *OvD*, paired oviducts; *Rec*, receptaculum seminis; *Te8*, eight tergites, reduced; *Stg*, spermathecal gland; *Spv*, spiculum ventrale; *Vag*, vagina.

ovaries (Ov) are present which are connected distally. The paired oviducts (OvD) are short and stout. The vagina (Vag) is distinctly shorter than the ovaries. Near the basal end of the latter two cement glands (Ceg) originate. They are rather weakly developed, short and ball-like in outline. A bursa copulatrix is not present. The receptaculum seminis (Rec) originates from the vagina at about the

same level as the cement glands; it has the shape of a pipe and bears on its distal end the spermathecal gland (Spg). The receptaculum was examined in all three species but no differences have been found.

In the classification of the *Scolytidae*, based on the female reproductive organs by Nuesslin, *Gnathotrichus* would fall in a group together with the genus *Thamnurgus* Eichhoff.

The Alimentary Canal

The alimentary canal was fully investigated in *Gn. materiarius* Fitch, the proventriculus in *Gn. retusus* Lec. and *sulcatus* Lec., also. The whole alimentary canal of *Gnathotrichus* is illustrated in figure 34, the proventriculus in figure 35.

The alimentary canal is a tube extending from one end of the body to the other. As in most of the mandibulary insects, three main divisions are clearly defined. These are termed the fore, mid, and hind intestine (fig. 34, A, B, C). The ectodermal origin of the fore- and hind intestine are well illustrated by the occurring chitinizations.

Fore-intestine.—On the fore-intestine the following consecutive divisions are well defined: The Pharynx (?), Oesophagus (Oes), Crop (Cr), and the proventriculus (Pve). The well developed proventricula are the characteristicum of the adults.

The pharynx is not distinctly defined from the mouth cavity.

The oesphagus is about as long as the crop and the proventriculus united. It consists of a simple tube, widened distally where it gradually passes over to the crop.

The strongly widened tube situated apically of the proventriculus may be designated as the crop.

Proventriculus.—The proventriculus is a highly specialized organ in which the food is prepared before it enters the more delicate ventriculus. The characteristic features of the proventriculus are a remarkable development of the chitinous intima into folds and teeth and a considerable increase of the size and development of the muscles of this region. On account of the importance of the proventriculus as a taxonomical characteristicum and of the general morphological interest of this structure, a more detailed discussion seems to be necessary.

Lindeman, who was the first investigator of the *Scolytid* proventriculus, distinguished two main parts or longitudinal divisions. The anterior part he called the Sack, the posterior, or caudad part, the Kaumagen. Nuesslin and Fuchs followed Lindeman's nomenclature. The Sack (Lindeman) corresponds to the crop (Hopkins) and forms the intermediate part between the oesophagus and the Kaumagen (Lindeman). Hopkins used the term proventriculus for the Kau-
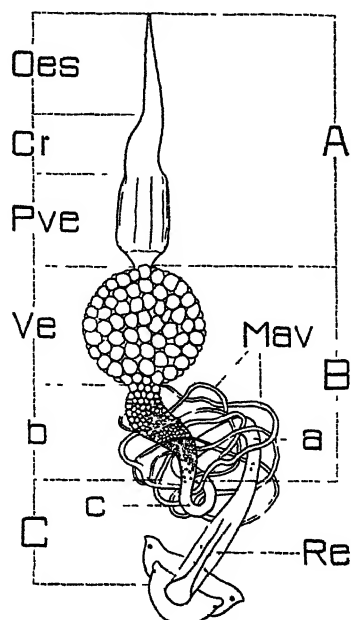
FIG. 34.—*Gnathotrichus materiarius* Fitch: Adult, alimentary canal and its appendages.

A, fore intestine; *B*, mid-intestine; *C*, hind-intestine; *Cr*, crop; *Mav*, malpighian vessels; *Oes*, oesophagus; *Pve*, proventriculus; *Re*, rectum; *Ve*, ventriculus; *a*, large intestine; *b*, posterior tube of the mid-intestine; *c*, small intestine.
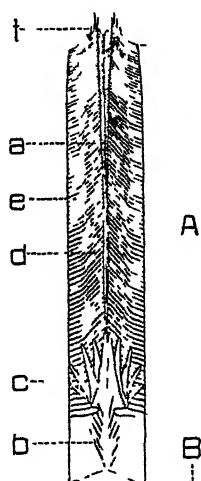
FIG. 35.—*Gnathotrichus materiarius* Fitch: Proventriculus.

a, median line; *b*, sutural teeth; *c*, anterior closing teeth; *d*, dentation of masticatory teeth, all together, masticatory brush; *e*, femora of the masticatory teeth, Abdachungszaehne (Nuesslin); *f*, posterior closing teeth; *A*, masticatory plate; *B*, anterior plate.

magen (Lindeman) only. In the following discussion the interpretations of Hopkins of the terms crop and proventriculus are used.

The proventriculus consists of eight plates arranged to form a tube, as illustrated in figure 35. On each plate two longitudinal divisions are clearly defined. Lindeman called the cephalad part the Plattenteil (A), the caudad part the Ladenteil (B); the corresponding terms of Hopkins are anterior plate and posterior or masticatory plate. The latter terms are adopted in this paper. In *Gnathotrichus*, both of these plates are divided by a median suture (a) which is distinctly visible on the masticatory plate and indicated by a row of bristles (b) on the anterior plate. These bristles, which are of taxonomic importance, have been called Zaehne am medianen Kauplattenrand by Nuesslin and sutural teeth by Hopkins. In *Gnathotrichus* they are present as slender, sharply pointed, and simple bristles. The anterior plate is not quite one-sixth as long as the whole proventriculus. The masticatory plate (A) bears a symmetrical arrangement of teeth which presents the true chewing apparatus of the proventriculus. On each tooth two elements are clearly defined, the instep and the dentation. The totality of the insteps corresponds to the Abdachung (c); that of all dentations to the Buerste (a) of the German authors. Hopkins called the first mentioned the femora of the masticatory teeth, the latter the masticatory brush. The masticatory teeth are all similar in shape and very numerous in the genus *Gnathotrichus*. Cephalad, they are bordered by a few (8-12) longer teeth (e) which differ greatly in shape and which are directed toward the center of the proventriculus. These teeth are apparently intended to regulate the entering of the food. They have been called Sperrborsten by Nuesslin and closing teeth by Hopkins. To distinguish them from a similar arrangement of teeth which occur in *Gnathotrichus* and other genera on the caudad end of the masticatory plate (f) it is proposed to call the former cephalad closing teeth, the latter caudad closing teeth. In *Gnathotrichus*, the following armatures are not present:

(a) Hackenzaehne (Nuesslin), or apical teeth of the anterior plate; the designation of a row of short, often curved teeth on the apical margin of the anterior plate.
(b) Ersatzperrborsten (Nuesslin), marginal bristles or marginal fringe (Hopkins); a longitudinal row of bristles along the lateral margin of the anterior plate.
(c) Kreuzlinie (Nuesslin), a row of short, stout teeth arising from the lateral margin of the anterior plate and converging posteriorly.

(d) Abdachungszaehne (Nuesslin), masticatory teeth which have two dentations, one, the totality of all composing the masticatory brush, and a second smaller tooth on the instep, the totality of which forms a second brush consisting of a single row of teeth only.

In the classification of the *Scolytidae* based on the proventriculus, *Gnathotrichus* should be placed with *Xyloterus* Er., *Xyleborus* Eichh., *Anisandrus* Ferr. and other ambrosia beetles together in one group. There is little doubt that the similarity of the digestive systems in ambrosia beetles of the Superfamily *Scolytoidea* is of no importance in the classification. These are merely parallel modifications of groups deriving from very different ancestors.

The proventriculus is very similar in all three species of *Gnathotrichus* and it is not possible to distinguish them by characters of this part.

Mid-intestine.—The mid-intestine is about one-third of the whole length of the alimentary canal. According to Nuesslin the proportions are the same as in *Anisandrus dispar* Fabr. and *Xyloterus lineatus* Oliv.

In *Gnathotrichus* two subdivisions of the mid-intestines are well defined. The anterior part, which presents the widest part of the whole alimentary canal, has the form of a ball and is covered with short, half spherical gastric coeca. This part is here designated as the ventriculus proper. The posterior, much narrower tubelike part, is here called the posterior tube of the mid-intestine. It bears much smaller gastric coeca which distinctly decrease in size toward the origin of the Malpighian vessels and which are always more filiform in shape. The origin of the Malpighian vessels marks the posterior limit of the mid-intestine. These are rather narrow, long tubelike vessels, strongly entangled around the posterior part of the mid-intestine and do not vary noticeably in size.

Hind-intestine.—While the fore- and mid-intestine are situated as a straight tube in the body, the hind intestine forms a distinct loop. The latter does not bear any gastric coeca but is characterized by the muscles which enclose it. The subdivisions, the small and large intestine and the rectum, are not so clearly separated. The ovaries of the female reproductive organs are always situated above the hind intestine; the testi of the male lie under and ventral to it.

THE LARVAE

On account of the difficulty in getting material of the western species, the following discussion is based on *Gnathotrichus materiarius* Fitch only.
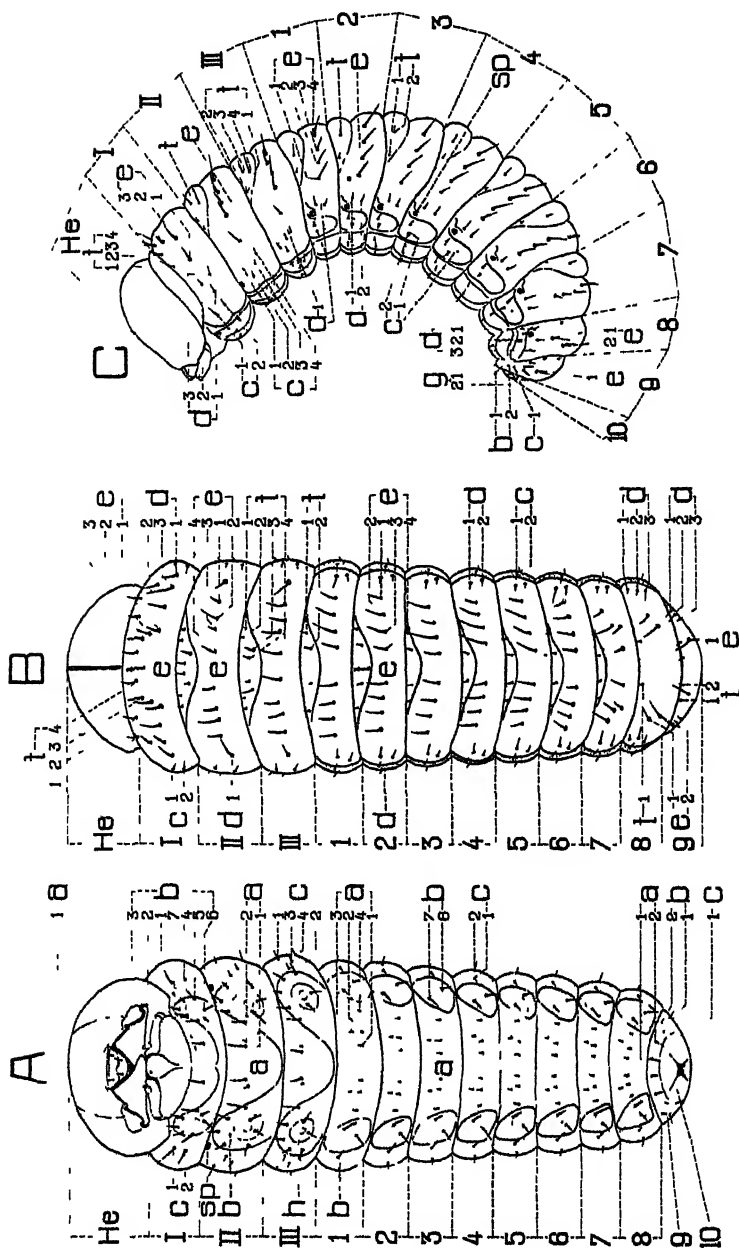
FIG. 36.—*Gnathotrichus materiarius* Fitch: Fully-grown larva, showing structure and arrangement of setae; A, ventral, B, dorsal, C, lateral aspect.

EXPLANATION OF FIG. 36.

He, head; *I, II, III*, the three thoracic segments; 1-10, the ten abdominal segments; a, sternal plate, seta sternalis; a_1, single seta on prothoracic sternum; a_{2-5}, two single setae on meso- and metathoracic sternum, and also on 9th abdominal segment; $a_{1, 2, 3, 4}$, four setae on abdominal sternum 1-8; b, sternellar plate, seta sternellaris; b_{1-5}, seven setae on the thoracic segments; b_{1-2}, two setae on the abdominal segments 1-9; c, hypopleural plate, seta hypopleuricum; c_{1-2}, two setae on hypopleurite of first thoracic segment and abdominal segments 1-7; c_{1-4}, four setae on hypopleurite of second and third thoracic segments; c_{1-3}, three setae on hypopleurite of eighth and ninth abdominal segments; c_1, one seta on hypopleurite of ninth abdominal segment; d, epipleural plate, seta epipleuricum; d_{1-3}, three setae on abdominal segments 8 and 9, and first thoracic segment; d_1, one seta on abdominal segments 2 and 3; d_{1-2}, two setae on abdominal segments 1-7; e, scutellar scutal plate, seta scutuli; e_{1-3}, three setae on thoracic segment 1; e_{1-4}, four setae on thoracic segments 1 and 2, and abdominal segments 1-7; e_{1-2}, two setae on abdominal segment 8; e_1, one seta on abdominal segment 9; f, prescutal plate, seta praescuti; f_{1-4}, four setae on thoracic segments 1-3; f_{1-2}, two setae on abdominal segments 1-7; f_{1-3}, three setae on abdominal segment 9; f_1, one seta on abdominal segment 8; g, anal lobes, anal segment; g_{1-2}, two setae on anal segment, seta analis; h, foot calli; sp, spiracles.

The structure and general appearance of the larva are shown in figure 36. The larva is legless, subcylindrical, white in color except the heavily chitinized and therefore reddish-brown headcapsula. The full grown larva is about 3.7 mm. long. Three thoracic and nine abdominal segments are well developed. The anal lobes may be regarded as a tenth abdominal segment. The three thoracic segments are nearly equal in size and only little larger than the first abdominal segment. The abdominal segments decrease slightly in width and length toward the apex. All segments and the head are armed with constant setae. The statement of Hopkins (38) that " with the exception of scattering hairs on the head and on the scutellar lobes of the thoracic and abdominal segments the body is without distinguishing vestiture " in *Dendroctonus* has been found to be not true. There occur at least in *Dendroctonus valens* distinct setae. That this is not exceptional in the *Scolytidae* has been proved by Russo (57) and the author. The latter has studied many species and has found that every examined species shows distinct setae. The following discussion is based on the full grown larvae only. The fact that the present study was made in a private home did not allow of rearing work and therefore the question of molds, etc., cannot be discussed at present.

THE CHITINOUS SKELETON

THE HEAD

The head of the larva is more simple in structural details than that of the adult. It is distinctly narrower than the first thoracic segment when seen from above, but nearly equal in length and in width to the latter when viewed from the side. The general structure is shown in figure 36, the anatomical details in figure 37. The more striking differences in the larval head are found in the presence of a clearly defined front, clypeus, labrum, and a well developed submentum.

Epicranial suture.—The sutura metopica as well as the sutura fronto-verticale are well developed and double lined (a, b). They are not raised or padded as in the adults.

Front.—The front (fig. 37, Fr) is triangular in outline, plano-convex and clearly defined by the epicranial suture. The lateral sides are bordered with six strong bristles each (d). These setae are here called setae fronto-lateralis. The base of the front is smooth without any armation.

In the discussion of the larval setae it seems to be very useful to compare the results obtained with those of other authors. From the

literature available, only two species have been found to be studied at the present. These are *Dendroctonus valens* Lec., investigated by Hopkins, and *Chaetoptelius vestitus* Fuchs studied by Russo. The
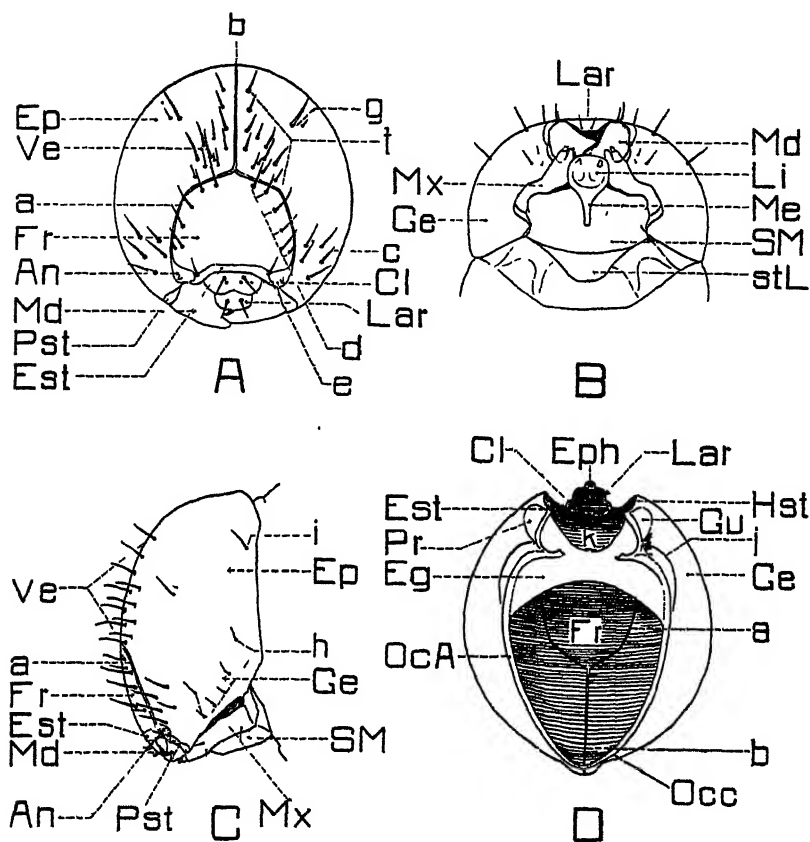
FIG. 37.—*Gnathotrichus materiarius* Fitch: Head of fully-grown larva; A, frontal aspect, B, ventral aspect, C, lateral aspect, D, occipital aspect.

An, antenna; *Cl*, clypeus, seta clypei; *Eg*, entogular plate; *Ep*, epicranium; *Eph*, epipharynx; *Est*, epistoma; *Fr*, front; *Ge*, gena; *Gu*, gula; *Hst*, hypostoma; *Lar*, labrum, setae labralis; *Li*, ligula; *Md*, mandible; *Me*, mentum; *Mx*, maxilla; *Occ*, occiput; *OcA*, occipital apodeme; *Pr*, pregena; *Pst*, pleurostoma; *SM*, submentum; *Ve*, vertex; *a*, sutura metopica; *b*, sutura fronto verticale; *c*, seta geno mediana; *d*, seta fronto lateralis; *e*, seta epistomalis; *f*, seta verto mediana; *g*, seta verto lateralis; *h*, seta geno lateralis; *i*, seta epicrano-lateralis; *j*, gular suture; *k*, maxillare foramen; *stL*, sternal lobe.

comparison of the setal arrangement with the latter species will be given at the end of each chapter.

Clypeus.—As mentioned before, the clypeus (fig. 37, Cl) is well developed in the larvae. It consists of a nearly rectangular plate which is heavily chitinized, distinctly emarginate anteriorly and broadly rounded antero-laterally. Basally it is separated from the

epistoma by a faint suture. A pair of bristles and two punctures occur near the basal margin. The setae are called setae clypei.

Labrum.—The labrum (fig. 37, Lar) is basally separated from the clypeus by a distinct suture. It consists of a heavily chitinized half circular plate. It is as long as, and about one-third narrower, than the clypeus and bears several papilla apically. Half way of its length occur two long bristles, the setae labralis.

Epistoma.—Between the front and the clypeus, a narrow thickened transverse band occurs which may be designated as the epistoma (Est). Laterally this structure is slightly bent forward and this part bears the dorsal articulation of the mandibles. On the latero-basal angles, near the suture, a long bristle is situated. The proposed name is seta epistomalis.

Pleurostoma.—A faint suture hems the lateral portion of the oral foramen, parallel to the lateral exposed part of the mandibles, which cuts off a narrow area of the cranium. This area, the pleurostoma, is slightly raised externally; internally it is ridgelike, and connects the epistoma with the hypostoma.

Hypostoma.—The hypostoma (fig. 37, Hst), which bears the ventral articulation of the mandibles, is rather ill-defined externally. Internally it is ridgelike and the articulatory condyles and fossa are submerged. Towards the occipital foramen it is extended in another ridge from which the connecting membranes of the maxilla and the submentum arise.

Occipital foramen.—The occipital foramen (fig. 6, Oct) is situated on the caudad face of the head capsula. It is heart-shaped and is bordered by a ridgelike rim, the occipital apodeme (fig. 37, OcA). The latter is interrupted ventrally. The entogular plate extends into the foramen under the occipital apodeme giving the open space of the foramen the shape of a triangle, the sides of which are broadly rounded.

Gula.—The gula (Gu) is present as two small lobes, each situated along the ventro-lateral angles of the occipital apodeme. The lateral limitation is indicated by an obscure suture.

Entogular plate.—A subchitinous plate (Eg) connects the genal areas and extends ventrally up to the hypostoma. It was called the entogular plate by Hopkins. The open space of the oral foramen is also reduced by the lammella-like extension of this plate. The entogular plate is not visible externally but hidden from the submentum.

Pregena.—A narrow area along the ventral extensions of the hypostoma, and laterally limited by obscure lines, may be considered as the pregena (Pr).

Other topographical regions of the cranium are not defined by sutures but they are somewhat limited by the occurring setae.

Vertex.—The area on both sides of the sutura fronto-verticale, the vertex (Ve), bears two groups of setae. Eleven bristles (f) are situated along each side of the sutura fronto-verticale. Four of them are arranged in a single row along the suture; the rest occur in the angle formed by the sutura fronto-verticale and the sutura metopica. They are called setae verto-mediana. A single bristle widely separated from the setae verto-mediana, the seta verto-lateralis (g) presents the second group. Sometimes a minute hair is also visible near the latter mentioned bristle.

Gena.—The area between the sutura metopica and the occipital apodeme ventro-laterally to the vertex is here designated as the gena (Ge). It bears two groups of setae, one on the level of, and close to, the antennae (c) and one laterally (h) to them but widely separated from them. The former consists of five, the latter of six long bristles. The corresponding names are the setae geno-mediana and the setae geno-lateralis.

Epicranium.—The area dorsally to the genae and laterally to the vertex is called the epicranium. A single bristle (i) sometimes associated with a minute hair, is situated near the occipital apodeme. It is called the seta epicrano-lateralis.

THE APPENDAGES OF THE HEAD

THE ANTENNAE

The antennae (fig. 37, An) are present as small membranous lobes next to the ventral end of the sutura metopica. Each bears one papilla and numerous minute hairs.

THE MOUTHPARTS

Mandibles.—The mandibles (fig. 28) differ somewhat from those of the adults, in contrast to which only one median tooth is present and the shape of the mandible is more slender and triangular. The setae are present in the same number as in the adults but their position in relation to each other is different. Proposed names: setae mandibulae dorsalis and setae mandibulae lateralis.

Maxillae.—The maxilla of the larva (fig. 38, A) is much simpler in structure than that of the adult. However, all parts present in the adult maxilla are also distinguishable in the larva.

The cardo (Ca) is present as a distinct sclerite, triangular in outline and connected with the extended hypostomal ridge, the mentum and the stipes respectively. This is, as in the adult, not the only con-

nection of the maxillae with the mentum. The subgaleal area is also connected with the mentum along its interno-lateral margin. The stipites (St) are distally not subdivided into a palpifer, and are fused internolaterally with the subgalea.

A single bristle (b) occurs near the externo-lateral margin. It was called the setole laterale dello stipite by Russo. In the present paper the name is modified into seta stipitis maxillaris. The palpiferal area
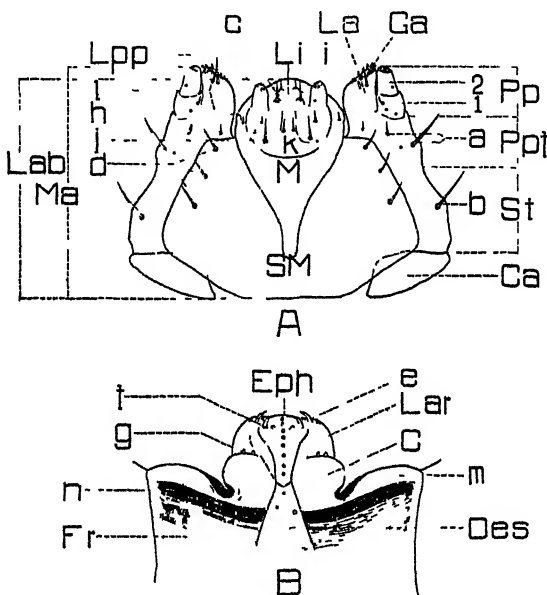
Fig. 38.—*Gnathotrichus materiarius* Fitch: A, labium and maxilla, ventral aspect: B, clypeus and labrum, ventral aspect.

Ca, cardo; *Fr*, front; *Eph*, epipharynx; *Ga*, galea; *La*, lacinia; *Lab*, labium; *Lar*, labrum; *Lpp*, labial palpi; *Li*, ligula; *M*, mentum; *Ma*, maxilla; *Oes*, oesophagus; *Pp*, maxillar palpi; *Ppf*, maxillar palpifer; *SM*, submentum; *St*, stipes; *C*, clypeus; *a*, seta palpifera maxillaris; *b*, seta stipitae maxillaris; *c*, seta ligulae distalis; *d*, seta submento-lateralis; *e*, papilla labro-apicalis; *f*, papilla epipharno-distale; *g*, papilla clypei; *h*, seta menti; *i*, seta ligulae mediana; *j*, seta labio-palpiferis, and palpiferal area; *k*, seta ligulae basalis, and basal area; *l*, seta lacinio-maxillaris; *m*, epistomal apodeme; *n*, apodeme between lateral angle of epistoma and dorsal angle of pleurostoma.

bears two bristles (a) and one puncture; the outer corresponds to the setola laterale dello palpifera, and the inner to setola mediana dello palpifera (Russo), here called seta palpiferae (maxillaris). The palpus is two-segmented, telescopic, the first segment armed with a short fine hair and two punctures, the second with punctures only. The bristle on the first segment is the setola palpiale (Russo) but to distinguish it from possible setae on other joints, it should be called seta palpo-maxillaris 1°. The lacinia is present as a well developed lobe distally armed with two long bristles (setae lacinio-maxillaris)

and a few papillae. The galea is largely fused with the lacinia. Distally a rather shallow fold indicates the separation of these two sclerites.

The setae of the maxillae have not been studied thoroughly enough to decide if they are of taxonomic importance or not. In *Dendoctonus valons,* no setae or punctures occur on the palpus and none of them on the lacinia, according to the drawings published by Hopkins. On the other hand it was found that the setal arrangement of

TABLE I.—*Setae of the head, nomenclature.*

Nomenclature of Dr. Russo	Used on	New nomenclature	Used on
Setole mediane-distale			
Setole submediane	Frons	Seta fronto-lateralis	Frons.
Setole laterali			
Setole basali	Frons-epistoma	Seta epistomalis	Epistoma.
Setole basali clypeali	Clypeus	Seta clypei	Clypeus.
Setole mediane distali			
Setole premediane	Labrum	Seta labralis	Labrum.
Setole sublaterali			
Setole basali-laterali			
		Seta verto-mediana	Vertex.
		Seta verto-lateralis	
Setole laterale del vertice			
Setole mediane	Genae	Seta geno-lateralis	Genae.
Setole basale			
Setole interna del vertice			
Setole della gena			
Setole mediane	Genae	Seta geno-mediana	Genae.
Setole esterna			
Setole basale			
		Seta epicrano-lateralis	Epicranium.
Setole dorsali	Mandible	Seta mandibulae dorsalis	Mandible.
Setola sublaterale-basale	Mandible	Seta mandibulae lateralis	
Setola laterale dello stipite	Stipes	Seta stipitae maxillaris	Stipes.
Setole mediane del palpifero	Palpifer	Seta palpiferae maxillaris	Palpifer.
Setole laterale del palpifero	First joint of palpus.	Seta palpo-maxillaris 1°	First joint of palpus.
Setole palpiale			
		Seta lacinio-maxillaris	Laciniae.
Setole distale			
Setole mediane	Submentum	Seta submento-lateralis	Submentum.
Setole subbasali			
		Seta menti	Mentum.
Setole subbasali	Mentum	Seta labio palpiferis	Palpifer of labium.
Setole distale	Ligula	Seta ligulae distalis.	
Setole mediane		Seta ligulae mediana.	
		Seta ligulae basalis.	

Gn. materiarius Fitch is exactly the same as that of *Chaetoptelius vestitus* Fuchs, illustrated and described by Russo.

Labium.—The labium (Lab) of the larva is very different in structure from that of the adult. Indications are that the labium of the larva as well as that of the adult will become more and more important as the bearer of taxonomic characters in the *Scolytidae.*

The submentum (SM) is present as a large sclerite and is trapezoid in outline. The shape is more like that of *Chaetoptelius vestitus* Fuchs. It is slightly chitinized, laterally connected with the maxillae and bears three pairs of setae (d), the same number and in a similar arrangement as in *Chaetoptelius vestitus* and *Dendroctonus valens.* Russo called these setae setole subbasale, setole mediane and setole distale in order proceeding distad. The anterior margin of the sub-

6

mentum does not extend as far as the origin of the palpi as in the two other species mentioned above.

The mentum (M) is a submembranous triangular plate the base of which is anterior. The posterior angle is narrow and strongly produced. Anteriorly it is fused with the palpiferal area of the labium. A single bristle and a puncture (h) are situated on the antero-lateral angles. The name proposed is seta menti.

TABLE II.—*Comparison of head setal arrangement.*

Seta	*Chaetoptelius vestitus* Fuchs.	*Dendroctonus valens* Lec.	*Gnathotrichus materiarius* Fitch.
Fronto-lateralis	4	4	6
Epistomalis	1	1	1
Clypei	2	1	1
Labralis	5	2	1
Verto-mediana	0	?	12
Verto-lateralis	0	?	2
Geno-lateralis	8	?	6
Geno-mediana	4	?	5
Epicrano-lateralis	0	?	1
Mandibulae-dorsalis	2	2	2
Mandibulae-lateralis	1	1	1
Stipitis maxillaris	1	?	1
Palpiferae maxillaris	2	?	2
Palpo-maxillaris	1	0	1
Lacinio-maxillaris	1	0	3
Submento-lateralis...........	3	3	3
Menti	0	0	1
Labio-palpiferis	1	1	2
Ligulae-distalis	1	1	1
Ligulae-mediana	0	0	1
Ligulae-basalis	1	1	1

The ligula (Li) consists of a circular plate largely surrounded by the mentum. From subdivisional parts the base of the ligula is visible from which it is well defined by faint sutures and the palpi (Pp). The base bears a single pair of setae. They are present as two short bristles and are called the setae ligulae basalis. The palpiferal area is situated on both sides of the base. The part anterior to the base of the ligula and between the palpi may be designated as the distad end of the ligula. The palpi are two-jointed. The palpiferal area bears two setae (j) which are called setae labio-palpiferis. The distal area of the ligula is armed with two pairs of setae. Proposed names: setae ligulae mediana and distalis.

THE THORAX

The thoracic segments are somewhat larger in size than those of the abdomen. They do not differ from each other in shape but are distinguished by the structure and the development of the setae. The thoracic segments are legless as in the whole superfamily but the foot calli are distinct.

Dorsally, the prothorax is distinguished from the other two thoracic segments by the lack of the suture which divides the prescutum (fig. 36) from the fused scutal-scutellar area. However, the prescutum is indicated by the corresponding setae. On the meso- and metathorax, the prescutum is present as a narrow transverse sclerite (f), near the anterior margin of which the prescutal setae (f_{1-1}) are situated. The scutum (e) and the scutellum are in all three segments fused. The pleural area is fairly well defined by a longitudinal fold ventrally. Latero-dorsally it is fused with the scutal-scutellar area. Another longitudinal fold divides the pleural area into two distinct parts. The part next to the scutal-scutellar area represents evidently the epipleurite (d), the ventral part the hypopleurite (c). The former has a smooth surface bearing setae only; the latter has the surface covered with minute spines beside the setae. On the sternum two subdivisions are plainly visible, the sternal (a) and the sternellar area (b). The sternellar area or sternellum consists of two large lateral lobes which are connected by a very narrow band medially. The lateral lobes which bear the foot calli are covered with minute spines similar to those in the hypopleurites. There is not enough evidence to speak about a poststernellar area in *Gnathotrichus* as it should be present in *Dendroctonus* according to Hopkins. The setal arrangement will be discussed with that of the abdomen.

THE ABDOMEN

The abdomen (fig. 36) consists of ten segments, the tenth of which is strongly reduced and present as the anal lobes. The segments decrease in size slightly towards the apex. Segments one to seven inclusively are alike in structure and setal arrangement. They differ in structure from the meso- and metathorax in having longitudinal folds which separate the epipleural area from the sternum and the scutal-scutellar area. Also the sternal-sternellar suture is restricted to a membranous fold. The two lateral lobes of the sternellum are apparently not connected medially. The eighth segment does not show signs of the prescutal-scutal suture. Still more reduced is the ninth segment; it has no sutures or folds but the different sclerites can be

determined very plainly from the position of the setae. The anal or tenth segment is separated from the ninth by an obscure suture. It consists chiefly of the four anal lobes. There is no difference in the structure of these lobes and also armations do not occur as in other genera.

THE SPIRACLES

Nine pairs of spiracles are present, eight of which are situated on the epipleurites of the first eight abdominal segments. The ninth spiracle is on the same sclerite of the prothorax very close to the mesothorax.

THE THORACIC AND ABDOMINAL SETAE

It was found that the setal arrangement is very constant from specimen to specimen. The number of setae varies in the different segments. The smallest number of setae was found to be present in the anal segment (2×2) and the eighth abdominal segment (2×11); the greatest number was borne by the meso- and metathorax (2×22). The number of setae in the different segments is best explained by

TABLE III.—*Setae of thorax and abdomen, nomenclature.*

Nomenclature of Dr. Russo	Used on the segments	New nomenclature	Used on the segments	Fig. 36
Setole tergali mediana..........	I, II, III, 1	} Seta praescuti	I, II, III, 1-9	t
Setole protergali	1-8			t
Setole posttergali	I, II, III, 1-8			
Setole tergali-laterali	1	} Seta scutuli .... {	I, II, III, 1-9 }	e
Setole tergali	9			
Setole epipleuri	I, 1-8	} Seta epipleuricum ... {	I, II, III, 1-9 }	d
Setole pleuri-sternali	9¹			
Setole tergali-pleurali	II, III,			
Setole ipopleurali	I, 1-8	} Seta hypopleuricum .. {	I, II, III, 1-9 }	c
Setole pleurali-sternali	9²			
Setole epipleuri	II, III			
Setole sternali-anteriori-externe..	1			
Setole sternali-posteriori-externe..	1			
Setole sternali-mediane	1			
Setole ipopleurale	II, III	} Seta sternellaris .... {	I, II, III, 1-9 }	b
Setole sternali-laterali	II, III			
Setole sternali mediane.........	II, III			
Setole sternali	1-8			
Not investigated	......	Seta sternalis	I, II, III, 1-9	a
Setole anali	10	Seta analis	10	g

¹ The two dorsal setae.
² The two ventral setae.

table No. III and figure 36. It should only be mentioned that the meso- and metathorax and also the abdominal segments one to seven are alike. The prothorax, the eighth, ninth and tenth abdominal segments differ considerably. It also should be noted that the first abdominal segment does not show any difference from the following one, as shown in *Chaetoptelius vestitus* Fuchs, according to Russo.

The nomenclature of Russo has been adopted to a great extent but several changes have become necessary as illustrated in table III.

TABLE IV.—Comparison of the arrangement of the setae of the thorax and abdomen.

In each segment group the three columns are: D = *Dendroctonus valens* Lec., C = *Chaetoptelius vestitus* Fuchs., G = *Gnathotrichus materiarius* Fitch.

	I			II			III			1			2–7			8			9			10		
	D	C	G	D	C	G	D	C	G	D	C	G	D	C	G	D	C	G	D	C	G	D	C	G
Seta sternalis		(?)	1		(?)	2		(?)	2		(?)	4		(?)	4		(?)	+		(?)	2			
Seta sternellaris		13(?)	7		11(?)	7		8(?)	7			2			2			2		(?)	2			
Seta hypopleuricum		4	2		4	4		4	4		2	2		2	2		2	2			1			
Seta epipleuricum		3	3		(?)	1		3	1		2	2		2	2		2	3		2	3			
Seta prescuti		1(?)	4		1(?)	4		1(?)	4		1	2		1	2		1	2		2	2			
Seta scutuli		5(?)	3		3	3		4	4		4	4		4	4		4	1		2	1		2	2
Seta analis																		4						

THE ALIMENTARY CANAL

The alimentary canal (fig. 39) of the larva shows some of the more primitive conditions of the highly specialized digestive system of the adult. It is about $1\frac{1}{2}$ times as long as the body. The same chief divisions as in the adult stage are clearly defined, but the proportions of the length of these are quite different. The fore-intestine occupies only one-ninth of the whole alimentary canal while the mid-intestine is

FIG. 39.—*Gnathotrichus materiarius* Fitch: Alimentary canal and its appendages of a full-grown larva.

A, fore intestine; *B*, mid-intestine; *C*, hind intestine; *Mav*, malpighian vessels; *Oes*, oesophagus; *Re*, rectum; *Ve*, ventriculus; *a*, region corresponding to crop and proventriculus; *b*, posterior tube of mid-intestine; *c*, large intestine; *d*, small intestine; *e*, reproductive canal.

enlarged to spread over five-ninths of the same length. The gastric coeca are small, the proventriculus absent and the Malpighian vessels are very strongly developed.

Fore-intestine.—The epipharynx (fig. 38, Eph) is well developed and projects distally slightly over the anterior margin of the labrum. It is distinctly defined from the labrum and clypeus; four papillae occur anteriorly and a row of sensory pores medially. The latter punctures are reduced to a single puncture in *Ch. vestitus* and are absent in *Dendroctonus valens.* according to the respective authors. The hypopharynx does not show any armature or sensory organs.

The oesophagus is a short tube of about equal diameter throughout. The caudad widened part, which is also encircled by strong muscles, may correspond to the united crop and proventriculus.

Mid-intestine.—The mid-intestine occupies the greatest area of the whole digestive system of the larva. The ventriculus is pearlike in shape, having the blunt end anteriorly. The gastric coeca are not so densely placed and are smaller than in the adult. The posterior tube is distinctly separated from the ventriculus. It gradually decreases in diameter towards the apex and bears on its caudad end the Malpighian vessels. These originate as a single tube and become divided shortly after their origin. Three pairs of vessels are present.

Hind-intestine.—As in the adults the hind-intestine forms a loop. The hind-intestine is encircled by ring muscles. The small and large intestines are not very distinctly separated from each other. More clearly defined is the rectum. The latter is distinctly wider than the rest of the hind-intestine, and the muscles encircling it are much more strongly developed.

From the anus originates a glandlike structure which is strongly widened distally. This evidently represents the ectodermal part of the reproductive organs of the adult. See also the discussion of the reproductive organs of the adult.

THE PUPAE

In the study of the pupa of *Gnathotrichus,* special attention was given to the changes of the setal arrangement from larva to pupa. The only illustration of a pupa of the *Scolytidae* showing the setal arrangement was found in the monograph of the genus *Dendroctonus* by Hopkins (38). It seems that Hopkins, who has usually overlooked the setae of the larva, did not realize the origin of the setae of the pupa, which he called spines. Russo, on the other hand, shows plainly the setae of the larva but has ignored those of the pupa. In fact, it is a difficult undertaking to study the setae of such small larvae or pupae. In *Gnathotrichus,* it is not possible to find the setae by working with a binocular but slides had to be made and those carefully examined under the microscope. The following discussion is illustrated by figure 40. The setae are only barely visible soon after the last molting of the larva. In the young pupa they are most distinct before the pupa starts to become the mature color, and they disappear gradually with the ripening of the adult.

FIG. 40.—*Gnathotrichus materiarius* Fitch: Pupa; A, lateral aspect, B, ventral aspect, C, dorsal aspect.

An, antenna; *Bl*, elytra; *Ep*, epistoma; *Epl*, epipleurite; *FL*, fore legs; *He*, head; *Hpl*, Hypopleurite; *HW*, hind wings, or metathoracic wings; *La*, labium; *Md*, mandible; *ML*, middle legs, or mesothoracic legs; *Msn*, mesonotum; *Msst*, mesosternum; *Mtn*, metanotum; *Mtst*, metasternum; *Mx*, maxilla; *Prn*, pronotum; *Prst*, prosternum; *Sp*, spiracle; *St*, sternum, 1-8, sterna of abdomen; *T*, tergum, 1-8, terga of abdomen; c_{1-9}, setae hypopleuricum; d_{1-2}, setae epipleuricum; c_{1-4}, setae scutali; f_{1-4}, setae prescuti.

THE HEAD

The elements of the adult and larval head are also recognizable in the pupa. The antennae are among the first parts to be fully developed. The mandibles, the maxilla and the labium are first indicated by low elevations which become gradually the shape of the corresponding elements in the adult stage. A lobe, situated dorsally of each mandible (Ep) is more distinct in the younger pupa and gradually disappears. It is apparently the reduced labrum and clypeus. A similar development takes place with the frontal groove which is a distinct wide groove at first and later on becomes reduced to the narrow simple sutura fronto-verticale. The larval setae of the head are all completely lost in the pupa.

THE THORAX

Prothorax.—The shape and the relative proportions of the prothorax resemble very much that of the adult. The sternum and the extreme anterior margin of the pronotum are more strongly developed at first. The latter is padded at first and densely covered with minute spines. The setae are all lost with the exception of those of the prescutum and the scutum. The setae f_{1-4} of the prescutum are arranged similarly as in the larva while f_8 is widely separated from the rest in the direction toward the caudal margin of the sclerite. The setae scutali e_{1-4} are, as in the larva, situated in a nearly straight transverse line near the caudad border of the pronotum. The arrangement of the setae shows that the pronotum of the adult belongs with its anterior three-quarters to the prescutum and that only the caudad narrow portion originates from the scutum. The spiracle is plainly visible in the young pupa and becomes covered by the caudad lateral angles of the pronotum.

Mesothorax.—The mesothorax is somewhat more strongly developed in the pupa than in the adult. The mesonotum is not overlapped by the pronotum and is present as a nearly rectangular plate extending the full width of the mesothorax. The only setae found were the e_{3-4} of the larval stage; they are in a position similar to that in the larva. The elytra are thicker than in the adult, the tracheal vein is well developed, and the articulation occurs along their whole bases occupying the greatest part of the pleural area.

Metathorax.—In the metathorax the scutum with the scutellar groove is first recognizable. The prescutum and the postscutellum or postnotum are indicated by two narrow transverse bands only. The scutum bears the setae e_{3-4} corresponding to the larva. The meta-

thoracic wings at first extend over the elytra. The pro- and meso-
thoracic legs are exposed, the metathoracic or hind legs are largely
hidden by the elytra and the hind wings. None of the legs show
remainders of the sternal setae of the larva as was found by Hopkins
to be the case in *Dendroctonus*.

All the setae of the thorax consist of rather fine hairs, the longest
of which are F_{2-4} of the pronotum.

THE ABDOMEN

The abdomen is that part of the body where the external changes
from larva to pupa are less pronounced. The united scutum and pre-
scutum, the pleuron and the sternum are defined by sutures or folds.
The pleuron is also subdivided into an epi- and hypopleurite.

There are eight tergites well developed. Tergites one to seven are
similar in form. The outline is nearly regular rectangular. The first
five of them have the same number of setae as well as setae developed
in a similar manner. The setae e_{1-4} are arranged in a transverse
line near the caudal border of the tergites. The seta e_2 is always
hornlike and enlarged with secondary hairs arising from it; e_1 is
always small and simple.

The area around e_2 is strongly padded, raised, more steeply slop-
ing externo-laterally and gradually decreasing towards the setae e_3
and e_4. In tergite six the setae e_3 and e_4 are of the same shape and
appearance as e_2 in the foregoing tergites. The corresponding setae
of the seventh tergite are also more strongly developed than the
others but never reach the size and development of seta e_3 in other
segments. The eighth tergite does not bear any setae.

The prescutal area is not defined by sutures or lines but the setae
f_{1-2} are visible near the anterior border of tergites one to seven
as minute hairs. They change neither in development nor in position
during the transformation from larva to pupa, but are completely
reduced on the eighth tergite.

Pleurites.—The pleural area is, as in the larval stage, subdivided
into two subdivisions, the epipleurites and the hypopleurites. Between
them are situated the spiracles. The epi- and hypopleurites are nar-
row transverse bands, strongly padded and densely covered with
minute spines. The epipleurites one to seven inclusive are similar in
shape and bear, as in the larva, two small hairs each. The only dif-
ferences are in regard to their position. In the larva these setae are
diagonal to each other; in the pupa, in a horizontal plane. The hypo-
pleurites are similar in shape and sculpture but bear only one hair

each. These setae are situated near the cephalad margin of the hypopleurites.

The eighth pleurite resembles even in the young pupa more that of the adult than of the larva. No subdivisional plates are visible and no setae occur. The spiracle is situated on the laterocephalad angle of the united tergo-pleural plate.

The caudal spine (Hopkins), most probably represents the only external remainder of the ninth abdominal segment of the larva and it is in the opinion of the author a greatly enlarged seta of the pleural area.

Sternites.—In the young pupa the same number of sternites occur as visible tergites, namely eight. The first two sternites are present as two short plates dorsal to the metasternum. They disappear when the pupa becomes older. The sternites three to seven are fully exposed and have the shape of small sclerites in the adults. The eighth sternite is visible as two half circular lobes which indicate the future development of the spiculum ventrale. None of the sternites bear setae and also no subdivisional plates are recognizable.

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TROPISMS AND SENSE ORGANS OF COLEOPTERA

(WITH TWO PLATES)

BY

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CONTENTS

INTRODUCTION

This paper is a continuation of a series of studies dealing with the tropisms and sense organs of insects, suggested by Dr. A. L. Quaintance, Associate Chief of the Bureau of Entomology. It is written as a complement to the writer's former paper (47) entitled "Tropisms and Sense Organs of Lepidoptera," and contains practically no information found in the former one, although, of course, the information which deals with the Coleoptera alone, is of a similar nature.

In the paper on Lepidoptera the original work dealt mostly with the codling moth, but since this species was not a favorable insect on which to experiment in the laboratory, the original plan for conducting tests was much curtailed. In the present study the experimental work has been expanded and the Mexican bean beetle (*Epilachna corrupta* Muls.), which first appeared in Takoma Park and Sligo, Md., in 1927, was selected to represent the Coleoptera, owing to its abundance and great economic importance. When tested to odor stimuli alone it also was found to be an unfavorable insect; but when the adults were allowed to come in contact with the substances to be tested as foods, the beetles clearly demonstrated their likes and dislikes; and when tested to light and gravity in a dark-room, the adults proved to be almost ideal for this purpose.

In order to obtain comparative results which could be treated statistically, new technique and apparatus were devised, and the more important experiments were repeated over and over under controlled conditions.

A. TROPISMS

The tropisms of Coleoptera will be discussed first and then the sense receptors.

I. PHOTOTAXIS, GEOTAXIS, AND THIGMOTAXIS

1. REVIEW OF LITERATURE

Information concerning the phototaxis, geotaxis, and thigmotaxis of beetles is limited. Publications pertaining to light traps are numerous, but papers concerning the geotaxis, thigmotaxis, and other phases of phototaxis are scarce. In regard to the reactions of beetles to wave length and intensity of light, the field is practically unexplored.

(A) GENERAL REMARKS

Loeb (37, p. 20) remarked that an imago animal may respond to light in one way, its larva in a different way. For example, an adult June beetle moves toward light and is called photopositive, whereas its larva moves away from light and is thus photonegative. He further said (p. 70-73) that mealworms (larvae of *Tenebrio molitor*) are photonegative and behave under red glass as they do in the dark; but under blue glass, just as they do in the light. They adhere closely to objects, being positively stereotropic or thigmopositive. They flee from moisture and seek dry spots. He believed that positive thigmotaxis (stereotropism) and negative phototaxis determine the habits of these insects, which live in flour, protected from the light. The behavior of cockchafers (*Melolontha vulgaris*) under red and blue glass is similar to that of mealworms. Loeb believed that negative phototaxis may cooperate, but that thigmotaxis is doubtless the chief factor concerned in causing the larvae of cockchafers to burrow in the ground. The same writer (p. 85-86) put coccinellid beetles in a wooden box which was then placed in a dark closet. After repeated tests these lady-beetles were always found at the top of the box, proving that they were geonegative.

Weiss (94) placed three species of lady-beetles at the base of a 15-foot pole, which they soon climbed. He believes that this behavior demonstrates negative geotaxis.

Wodsedalek (97) has demonstrated that the phototactic responses of certain dermestids vary at different life-history periods. The larvae of *Trogoderma tarsale* immediately after hatching are photonegative. Negative phototaxis persists throughout the larval period, and even for a short time after the adults mate. Soon after ovipositing, the females become gradually indifferent to light and later become photopositive.

Breitenbecher (7) experimented with potato beetles, under dry and moist conditions, to ascertain what their tropic responses would be in a desert. When the beetles were confined in a moist medium, they were found to be photopositive and geonegative; but when desiccation resulted in a dry medium, they were photonegative and geopositive.

Runner (69, p. 25) tested tobacco beetles with color screens or ray filters which transmitted practically monochromatic light rays. He remarks that these beetles, in common with other insects, reacted most strongly to colors of shortest wave length. The movement toward blue or blue-violet was most pronounced, and the movement toward red least of all. These beetles, like other insects reacting negatively toward intense sunlight, were only slightly sensitive to light at the lower end of the spectrum, and rays of longer wave length, limited to red and orange, seemed to act on them in much the same manner as darkness. Beetles exposed to bright sunshine under color screens of red and blue were observed to collect under the red screen almost as readily as they did when an opaque screen was used instead of the red, although the apparent intensity of light under the two screens was the same.

Smith (75) remarks that the larvae of the Japanese beetle are thigmopositive to living roots, and if these are not available, they adhere to stones, sticks, or the bottom and sides of the breeding cage. The adult beetles apparently can see colors, particularly green. This is taken advantage of by painting the bait traps green and by using green lead arsenate (78).

Moore and Cole (56) report that Japanese beetles collect in great numbers at the tops of trees, bushes, and weeds. This is caused by two tropic responses—positive phototaxis and negative geotaxis, which determine the head-tail orientation of the body. In the field and laboratory certain degrees of heat and light are necessary to cause active movements. These writers further say that since a geotactic response is shown by the beetles only when they are illuminated, it therefore follows that their movement in a lighted field is the result of three factors—negative geotaxis, photokinesis, and positive phototaxis. The first is constant, while the other two factors are functions of the

intensity of the illumination. Moore and Cole conducted many tests by confining Japanese beetles in a specially constructed wire-screen cage. Five light intensities were used in securing the reaction time of the beetles. The results obtained are presented in tables and graphically. Their summary is about as follows. Light and temperature above 23° C. are necessary to cause activity in the Japanese beetle. The effect of light as indicated by the rate of locomotor responses was related to light intensity according to Fechner's expression of Weber's law.

Richmond (67) devised an apparatus to determine the value of color and intensity of light. Over 100 tests were conducted, using Japanese beetles, but no definite conclusions were drawn from the results obtained.

Crozier (12) states that when creeping mealworms are tested to light rays, a definite intensity of white light (about 136 m. c.) is required to produce negative orientation away from contact with a vertical glass surface. This gives a measure of stereotaxis in terms of phototaxis, or vice versa. The effectiveness of light for the suppression of stereotaxis varies with the wave length. By determining the minimum energy required to inhibit stereotaxis with the different regions of the spectrum, it was found that the maximum effectiveness was sharply localized in the neighborhood of 535 millimicrons. The same author (11) conducted other experiments to show that mealworms, while creeping, exhibit homostrophic responses and stereotropic orientation to lateral contacts. Crozier finally concludes that stereotropism is truly a tropic character.

<center>(b) LIGHT TRAPS FOR BEETLES</center>

Artificial light as a control measure was probably first used in 1787 for attracting vine moths in Europe. Since that date light traps have been gradually developed and improved until today there are many types and varieties of gasoline, kerosene, acetylene, and electric lamps used for this purpose. Most of these have been devised primarily for catching Lepidoptera, but many beetles also are caught in them, and other traps are designed primarily for Coleoptera. It seems that none, however, has given complete satisfaction as a control measure.

Since 1914 Jarvis and his co-workers (28, 33, 35) have been devising light traps to catch sugarcane beetles in Queensland, Australia. Their object has been to develop a trap so simple that it might come into general use in sugarcane-growing regions. A very successful trap has finally been developed. It consists of a large pan about a yard square, with sides about 4 inches high, and of an ordinary acetylene

lamp. In Cuba, Barreto (5) reports that light traps are an effective means of dealing with other species of sugarcane beetles.

For many years light traps have been used for catching May beetles (*Lachnosterna*), but it is still doubtful whether this method, as a control measure, is really worthwhile. Sanders and Fracker (70) in Wisconsin used gasoline lantern traps to collect May beetles. Results were obtained concerning the distribution of species over a comparatively limited area, the optimum temperature for flights, and the most favorable location and arrangement of the light traps. Seventeen out of the 19 species known to occur in Wisconsin were caught in the traps. Van Zwaluwenburg (91) reports that in Porto Rico large numbers of May beetles were caught by means of a 400-candlepower gasoline lamp, and that the use of light traps should constitute a valuable means of control. Harned (22) reports that, in pecan orchards in Mississippi, where trapping May beetles at night by lanterns placed over tubs of oil and water has been practiced for many years, their numbers have been considerably reduced, and they appear to have caused less damage there than in previous years.

Runner (69, p. 49-51) reports that the tobacco beetle may be attracted to light traps in tobacco factories or warehouses and large numbers of them destroyed. An efficient trap can be made quickly and easily by pinning sheets of sticky fly paper around an electric light. Other types of light traps are discussed. One consists of a large globe connected with a cyanide jar; another, of a light and a shallow pan of oil; another, of a suction fan and a light; and another method is to collect the beetles at windows. Some of the beetles caught were examined for the purpose of determining their sex; nearly two-thirds proved to be females.

Smith (77) reports that light traps, placed over large funnels, have proved effective against the adults of the Asiatic garden beetle (*Aserica castanea* Arrow). In one instance as many as 157,774 beetles were caught in one trap during a period of 30 days.

For several years Williams (96) has been developing and improving light traps for insects. At last he has perfected one which has been proved successful. The source of the light is acetylene or electricity, and the killing agent is carbon tetrachloride or potassium cyanide.

In New York State, Collins and Nixon (9) have just published a second report concerning an investigation conducted on a large scale, in which 105 water-pan electric-light traps were installed in an orchard. Most of the insects caught were Lepidoptera, but incidentally many beetles were trapped. The method recently employed by Hermes .

(23) in California is also recommended to future investigators. He used large electric lights in an orchard to attract codling moths.

Gourdon (20) states that ultra-violet rays have been found to attract both diurnal and nocturnal insects. The rays appear to produce in the insects a sensation which is at first agreeable, but which soon becomes dangerous, if not fatal; in certain cases they are immediately blinded. A trap for use in vineyards, orchards, or fields is described, to which insects are attracted by means of ultra-violet rays, and are either drawn by the suction of an electric fan into a metal basket or fall blinded outside the trap, where they become an easy prey to birds.

Many more references on light traps are cited in " The Review of Applied Entomology, Series A," but perhaps enough has been said to convince the reader that this method of control is worth further investigation.

2. ORIGINAL WORK ON MEXICAN BEAN BEETLE

(A) RESPONSES OF LARVAE AND ADULTS TO DAYLIGHT

When the sun is shining brightly on warm days, larvae and adult bean beetles are rarely seen exposed to the direct sunshine in bean patches. During cloudy days and early in the morning many may be seen on the upper surface of the leaves, but most of them at all times live and feed on the under surface.

When brought into the laboratory most of them move toward the windows, being photopositive, while occasionally one moves away from the light, thus being photonegative. When tested in a phototactic box, 18 inches long, 12 inches wide, 12 inches high, and lined with a dead-black cloth (fig. 1), their responses were similar to those of codling-moth larvae, recently described by the writer (47, pp. 12-13). This box lay on a table by a south window in bright light, although not in direct sunshine. Dozens of insects were placed in it and the tracks of most of them were traced with a lead pencil. Larvae of the first and second instars were found to be weakly photopositive or indifferent to light. Many moved slowly, bending to the right and left, in any direction as if searching for food, while a few moved in circles toward the light (fig. 1, a and b).

Most of the larvae of the third instar were strongly photopositive (fig. 1, c), while the remainder were weakly photopositive or indifferent to light. The more active larvae of the fourth instar were usually strongly photopositive, but a few were indifferent. The less active ones were usually strongly photonegative (fig. 1, d). It was

later ascertained that most of the larvae, when about ready to pupate, became photonegative. These were sluggish in action, were deeper yellow in color, and their intestines usually were not visible through the integument as they are in the more active larvae.

Hundreds of adult bean beetles, including the overwintering ones, those of the second and third broods, and many ready to hibernate, were tested in one way or another. Practically all were found to be photopositive, most of them being strongly so (fig. 1, *e*). At no time were photonegative beetles observed. The nearest approach to this
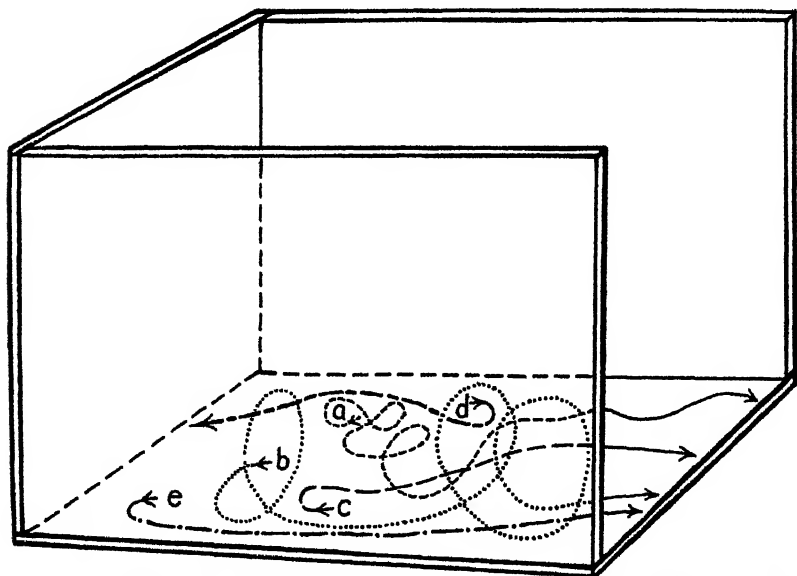

FIG. 1.—Diagram of phototactic box and tracings of tracks of Mexican bean beetle, illustrating responses to light of this insect. The tracings are as follows: *a*, larva just hatched; *b*, larva of second instar; *c*, larva of third instar; *d*, larva of fourth instar; and *e*, adult ready to hibernate.

condition was found among old ones of the second brood, but when repeatedly tested it was decided that they too were still photopositive.

(B) DESCRIPTION OF DARK-ROOM AND APPARATUS

Since it is often difficult to separate phototactic responses from geotactic ones, special apparatus is then necessary. Not having a dark-room whose temperature and relative humidity could be controlled, an attempt was made to construct one by using a room, 10 feet long, 9 feet wide, and 9 feet high. It was made totally dark as follows: Boards were nailed to the wooden shutters which closed

snugly, and then a dark green window shade (fig. 2, A) was pulled to the bottom of the window. The door (*B*) was made light-proof by fastening strips of black cloth around all its edges, and its transom
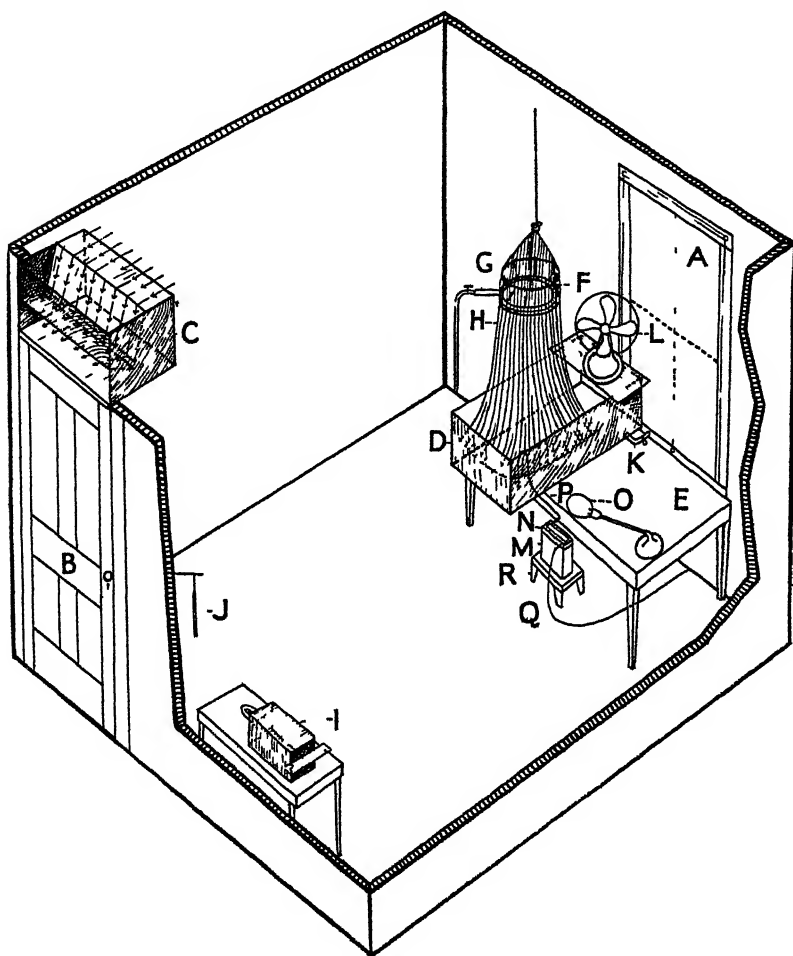
FIG 2—Diagram of a constant temperature and humidity dark-room, showing parts of room and apparatus used in testing photo-geotactic responses of Mexican bean beetle. The parts and apparatus are as follows *A*, window shade; *B*, door; *C*, ventilator; *D*, box; *E*, table; *F*, lawn sprayer; *G*, garden hose; *H*, bath towels; *I*, hygrothermograph; *J*, thermometer; *K*, outlet water pipe; *L*, electric fan; *M*, photo-geotactic box, *N*, water screen; *O*, electric lamp; *P*, siphon running to water screen; *Q*, siphon running from water screen; and *R*, stool.

was changed into a ventilator (*C*) through which air passed freely, but no light. The temperature and humidity were partially controlled by the following means. A box (*D*), 40 inches long, 24 inches wide,

and 12 inches high, lay on a table (E) by the window at the south end of the room. A wire frame-work, supporting a circular lawn sprayer (F), was suspended from the ceiling directly over the box; and a garden hose (G), running to a water spigot, was connected with the sprayer. Two large bath towels (H), put around the frame-work above the sprayer reached half-way to the bottom of the box, which was kept two-thirds full of water. A hygrothermograph (I) lay on another table at the north side of the room, and near this table there was a centigrade thermometer (J) the scale of which was marked in fifths of degrees. Before starting an experiment in this dark-room, water was turned on at the spigot, passed upward and outward from the spray, struck the bath towels, ran down them into the box, and finally passed through a pipe (K) to the outside of the room. In order to have good ventilation and a more humid atmosphere, air from an electric fan (L) was directed against the wet towels and water in the box. If the temperature and relative humidity could not have been satisfactorily controlled for the tests planned, the original idea was to use ice and water in the box for cooling the air, and a stove for heating it. Since small variations in temperature and relative humidity did not seem to affect the responses of the bean beetle, the ice and stove were not used.

Experience showed that the temperature and relative humidity inside the dark-room were influenced only slightly by outside climatic conditions. During the forenoons the temperature was often held nearly constant, and never varied more than two degrees centigrade, but during the afternoons the variation was usually larger. Table 1 shows that the greatest variation of temperature, between 9:00 o'clock a. m. and 4:30 o'clock p. m., was 4.2° C. and the smallest variation was 1.8° C. When the outside relative humidity was exceedingly high, water was not run through the sprayer, because it made the inside humidity too high.

The testing apparatus consisted of a tall box (fig. 2, M and fig. 3), a shallow water screen (N), and a lamp (O). The inside dimensions of the box (fig. 3, A), called a photo-geotactic box, were 12 inches by 5.5 inches by 1.75 inches. It had two sets of shutters, one of glass (a) and the other of wood (b), which fitted snugly in slots. The four sides inside the box were covered with a dead-black cloth, while one of the glass shutters was covered with cheesecloth. The inside of the box was marked with white lines into ten equal sections, numbers 1 to 10. When all four shutters were in place it was almost totally dark in the box.

The inside dimensions of the water screen (fig. 3, B) were 6 inches by 2 inches by 0.25 inch. The two pieces of glass (c) were held securely one-fourth inch apart by a strong wooden frame (d). The running water passed through a siphon (fig. 2, P) and a glass tube (fig. 3, B, e), having a bore of one-eighth inch, into one end of the water screen and out again at the other end through another tube and siphon (fig. 2, Q, fig. 3, B, f).
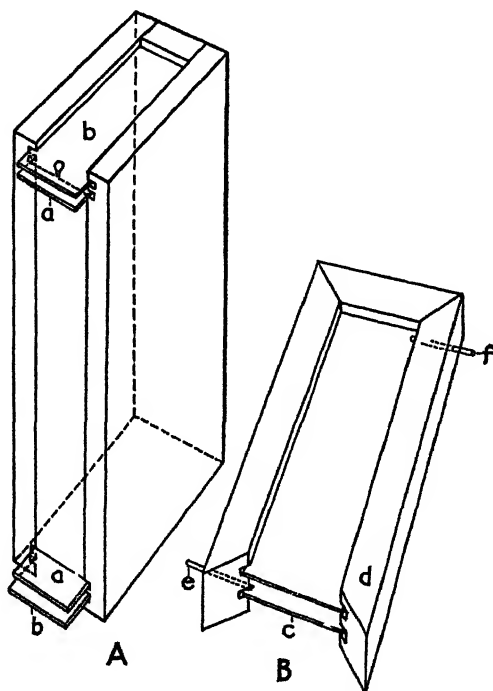
Fig. 3.—Diagrams of photo-geotactic box (A) and water screen (B), showing following parts of them: a, glass shutter; b, wooden shutter; c, piece of glass; d, wooden frame; e, inlet glass tube; and f, outlet glass tube.

The lamp (fig. 2, O), consisting of a blue daylight bulb 100 W, 110 V, rested on the table (E), or on a box, while the photo-geotactic box and water screen lay on a stool (R).

(c) RESPONSES OF ADULT BEETLES AND THEIR LARVAE IN DARK-ROOM

Since the writer was not able quickly and accurately to separate the live bean beetles according to sex, sex was disregarded in all the tests conducted. The beetles, otherwise, were selected so that those in each set were of practically the same age and responded to daylight readily.

After the temperature and relative humidity in the dark-room had become nearly constant, both shutters at the bottom of the photogeotactic box were inserted and 25 adult beetles were then put in the box on the cloth-covered glass shutter, after which the glass shutter at the top of the box was inserted, and finally the testing apparatus was assembled as shown in figures 2 and 3. The blue electric light bulb was then placed 10 inches directly above the water screen, which prevented the infra-red or heat rays from the light from reaching the insects. After a period of 15 minutes the wooden shutter was removed and the box was gently raised and turned toward the light so that the observer could see through it from end to end. The position of the beetles in the ten sections was then quickly noted and recorded in a table.

In test number 2 the beetles were again put in the bottom of the box on the cloth-covered shutter, but this time the box was gently turned upside-down and rested on the water screen, 10 inches below which was the light. In this case the beetles clung to the cloth and did not fall when turned upside-down. During the same forenoon tests number 1 and 2 were repeated alternately three times, and finally the results obtained in the two sets, each consisting of four tests, were treated statistically and recorded in table 1.

To secure a frequency distribution the responses were given values ranging from 1 to 10, corresponding to sections 1 to 10 in which the 25 insects were counted at the end of a test. If all 25 insects remained in section 1, the total value would be 25, or 1 as an average; and if all moved to section 10, the total value would be 250, or 10 as an average; but neither one of these extremes was actually observed, because the insects were always counted in two or more sections. To secure the arithmetic mean, which in each test lay somewhere between 1 and 10, the total value was divided by 25, and since each set of experiments consisted of four tests the frequency curve was represented by only four means. Owing to the small number of statistical items, Bessel's formula

$$\left(P.\,E.\ m = \pm 0.6745 \sqrt{\frac{\Sigma d^2}{n(n-1)}} \right)$$

was used to calculate the probable errors.

The values were accurate for those insects counted in sections 2 to 10, but not so for those counted in section 1, because they may have responded little or none, although most of them had left the cloth-covered shutter on which they were put. Consequently, the mean positions given in table 1 under the headings "up" and "down"

TABLE 1.—*Tests to determine differences between phototactic and geotactic responses of Mexican bean beetle, with and without use of light*

Stage of insects tested	Phototactic and geotactic responses combined (100 watt light used)			Geotactic responses alone (No light used)			Number of tests	No. of set	Temperature C°	Relative humidity	Date
	Mean position of insects forced		Difference	Mean position of insects forced		Difference					
	Up	Down		Up	Down						
Over-wintering beetles...	8.21 ± 0.041	5.81 ± 0.113	2.40 ± 0.120	8.05 ± 0.156	2.78 ± 0.083	5.27 ± 0.177	4	4	26.4–29.0	89–93	June 17
	7.75 ± 0.224	4.92 ± 0.337	2.83 ± 0.405	7.49 ± 0.309	2.01 ± 0.113	5.48 ± 0.320	4	5	26.0–29.2	90–93	June 20
	9.42 ± 0.065	6.98 ± 0.176	2.44 ± 0.188	7.98 ± 0.062	2.35 ± 0.108	5.63 ± 0.124	4	6	26.0–30.2	92–95	June 21
General average of above.	8.46 ± 0.072	5.90 ± 0.120	2.56 ± 0.140	7.84 ± 0.106	2.38 ± 0.055	5.46 ± 0.119	12	4 5 6			
Old beetles of 2nd brood...	7.41 ± 0.188	6.48 ± 0.039	.93 ± 0.190	6.31 ± 0.688	2.25 ± 0.173	4.06 ± 0.709	4	15	24.5–26.6	93–96	Aug. 19
Larvae of third instar....	2.24 ± 0.087	2.14 ± 0.059	.10 ± 0.105	2.28 ± 0.118	1.41 ± 0.098	.87 ± 0.153	4	4	24.0–25.8	86–88	June 26
Larvae of fourth instar..	9.05 ± 0.177	6.42 ± 0.192	2.63 ± 0.261	2.25 ± 0.149	1.47 ± 0.151	.78 ± 0.212	4	5	23.0–27.0	84–87	June 27

are slightly too high for those insects which did not respond readily; but the figures given under the heading " difference " are practically the same as those when all the insects counted in section 1 were eliminated.

Usually during the afternoon similar tests were conducted four times, using the same beetles, but no light was used. In this case, without the use of light, the geonegative response was 5.27 ± 0.177 more than the geopositive one, while with the use of light it was only 2.40 ± 0.120 more (table 1), 10.00 being equal to a 100 per cent response.

On later dates the preceding tests were again repeated, using two other sets of overwintering beetles. The general average and probable errors of the three series were therefore obtained by using the 12 means and the mean of them. Thus, for active, overwintering beetles the geonegative response, when light was used, was 2.56 ± 0.140 more than the geopositive one; but when no light was used, it was 5.46 ± 0.119 more, indicating that when the beetles were forced downward by the light this stimulus overcame about one-half of the geotactic one. In two of these series of tests the light was used during the forenoon, but in the third series during the afternoon. The sequence in which these insects were tested, therefore, had little or no effect on the results obtained.

The preceding tests were repeated by using one set of old beetles of the second brood. These insects were not so active as they were when younger and did not respond so readily to light and gravity as did the more active overwintering beetles. Their lower responses were due mostly to the fact that the insects soon became tired of being forced to respond.

Two sets of larvae were likewise tested in the photo-geotactic box and were found to be photopositive and geonegative (table 1). Compared to the adults they were sluggish and three times in four did not respond as readily to light and gravity. Larvae of the third instar reacted weakly to light and gravity, while the larvae of the fourth instar responded strongly to light but weakly to gravity.

The reader has doubtless noted that the writer has designed his experiments and discussed his results from the point of view that rate of movement is a measure of tropic response. After an animal is oriented, some writers claim that the rate of its movement toward or away from the source of excitation is not a measure of its tropic response. If a tropic response includes nothing more than the mere act of orienting, the preceding results then have little to do with the subject of tropisms. The writer in various publications has dis-

cussed the subject of tropisms from a broad point of view, and has not yet accepted any definition nor does he know exactly what a tropic response includes, but he believes that it includes more than orienting in a certain direction.

In conclusion, bean beetles and their larvae are usually found on the upper portions of their host plants, because they are photopositive and geonegative; but since direct sunshine in warm weather is harmful to them, they are usually found on the lower surface of the leaves.

II. CHEMOTAXIS

I. REVIEW OF LITERATURE

Most of the information regarding chemotaxis found in the widely scattered literature pertains to the subject of baits. Scores of references have been consulted, but only the more important ones will be cited.

(A) BAITS FOR WIREWORMS AND TENEBRIONIDS

It is not known when the practice of using baits for beetles was first begun, although this is an old control method. The Japanese growers, according to Treherne (85), were probably the first ones to use baits for catching wireworms, the larvae of elaterid beetles. After roasting dry rice shorts or rice bran, the Japanese then moistened the roasted material with water and made it into small balls, which had a strong odor said to be attractive to wireworms. The Japanese claimed that a single ball would catch 100 or more wireworms, but when this method was tested by Treherne a single bait buried in heavily infested soil never yielded more than 90 larvae.

Treherne (86) also tells about the old-fashioned way of attracting wireworms, which is still recommended as one of the few control measures. Pieces of cut potatoes, to which white wires have been attached, are buried in the infested soil. Upon visiting the infested area the potatoes are pulled from the ground by means of the wires, the wireworms are removed and destroyed, and then the potatoes are buried again. In Canada attractive baits, consisting of potatoes, balls of dough, shorts, meal, or rice bran, are set in the soil. The addition of molasses or other attrahent ("attractant") in these bran baits does not improve their attractiveness, nor has the inclusion of arsenicals been of any practical value.

Weldon (95) reports that small pieces of potatoes were planted between rows of beans in California. This bean crop was saved, while 30 acres of beans nearby, not thus protected, were entirely destroyed.

Borodin (6) reports that in Russia the best remedies for wire-worms are various baits, consisting of sliced potatoes, carrots, beets, oil cakes, cabbage stalks, etc., buried 3 or 4 inches in the soil. Those poisoned with Paris green or arsenic need no further attention. The unpoisoned ones must be inspected weekly. Poisoned maize baits are also recommended.

French (15) says that in Australia poisoned baits consisting of cut-up turnips, carrots, etc., soaked in lead arsenate, have given good results.

Lovett (38) states that in Oregon poisoned-bran mash may be placed under stones or boards in the fields as a control measure for wireworms.

Masaitis (39) reports that in Siberia baits of horse dung, poisoned with sodium arsenite, appeared to be considerably more effective than those of poisoned linseed or hempseed cake.

More recently special attractants have been given serious attention. Comparative tests, conducted in Washington State by Spuler (83), in which rice flour, graham flour, graham flour and sugar, bran, graham flour and oranges, graham flour and lemons, potatoes, carrot roots, carrot tops, and apples were used as baits gave a descending order of attractiveness as listed. Other tests, in which baits consisting of germinating Alaska peas, beans, corn, graham flour, and potatoes were used, indicated that the seeds and flour were about equal in at-tractiveness, but that the potatoes were far inferior. For practical control work use baits, particularly germinating seeds, to allure the wireworms to definite spots, and then the worms may be easily killed with a soil fumigant, such as calcium cyanide. When the worms have gathered around the bait, spaced about four feet apart, to partake of the feast prepared for them, all that remains to be done is to bury a little of this granular fumigant near the bait. Shortly the deadly fumes send the banqueters to their happy hunting ground and all is ended.

Federal entomologists (1) at Clarksville, Tenn., have recently made an interesting discovery in connection with poisoned-bran bait fed to tobacco wireworms, which have hitherto stubbornly resisted all efforts at direct control. These worms were easily attracted to bait flavored with ordinary nitrobenzene. In five series of large-scale ex-periments in tobacco fields these worms were reduced from 50 to 60 per cent by the use of this chemical as a bait flavoring. Other en-tomologists (2) at the Florida experiment station remark that a flavoring of nitrobenzene added to poisoned-bran bait is very attrac-tive to a variety and large range of insects, and they found it quite

attractive to the celery leaf-tier. If it is attractive to such diverse insects as wireworms and caterpillars it is quite possible that it will be found of value against a large number of insects.

Melander (50) states that a dough made of flour or bran proved very attractive to wireworms, but the addition of sugar, oranges, lemons, etc., added little to the drawing power of the baits.

Since the larvae of certain tenebrionid beetles are destructive, why not attack the evil at the source by destroying their parents? This was the way Wakeland in Idaho reasoned during the season of 1921. After discovering that these beetles feed greedily for a month before egg-laying time, he next found out that they could be easily killed during this period by feeding them poisoned-bran bait, thus largely eliminating them before they had a chance to start a new generation. The following season he (93) continued his experiments and states that the bait used consisted of bran, Paris green, amyl acetate, and water. It was distributed broadcast or in the bottom of furrows, plowed at regular intervals, over an area of 18,000 acres. This method is said to be practical and economical, because the beetles were effectively killed at a cost of about two and a half cents per acre for materials, and the labor involved was not a large item.

In 1920 Jack (29) in Rhodesia poisoned the adults of certain tenebrionids by using the bait recommended against cutworms.

Swenk (84) remarks that a promising remedy against the adults of *Eleodes opaca* is a bait prepared by mixing, dry, 25 pounds of coarse wheat bran and 1 pound of Paris green, to which is added ¾ ounces of amyl acetate in enough water to make a stiff mash. This quantity is sufficient for several acres when put in furrows.

Other species of tenebrionids in the United States (8), Russia (73), and Rhodesia (30) are more or less controlled by poisoned baits. In Southern Rhodesia several formulas have been used (31) successfully against so-called wireworms (tenebrionids). One of them is made of chopped green stuff, dipped in a solution consisting of 1 pound of sodium arsenite, 8 pounds of cheap sugar or 1 gallon of molasses, and 10 gallons of water. This bait may be broadcast or applied like bran bait.

(B) BAITS FOR STRAWBERRY-ROOT WEEVILS

During the past 25 years strawberry growing in the western parts of Washington, Oregon, and British Columbia has been handicapped by strawberry-root weevils. For 20 years or more many efforts have been made to develop a remedy for this serious pest, but not until recently has a satisfactory control measure been discovered. An

attractive poisoned bait was developed by M. J. Forsell of Seattle, Washington, who, at the suggestion of the present writer, attacked the problem through the weevil's sense of smell. In the preliminary experiments dried ground apples were found to be the most attractive substance tested, and magnesium arsenate was the most satisfactory poison. It is further claimed that the discovery and perfection of this bait marks an important horticultural step in the fruit industry of the State of Washington, as these weevils had become so serious in many places that the strawberry-growing industry seemed doomed.

Melander and Spuler (51) report their results concerning the poison-bait remedy for the strawberry-root weevils in Washington. They say that these destructive weevils can be satisfactorily, economically, and practically controlled by the distribution of a poisoned bait immediately at the close of the berry harvest. This bait consists of sun or oven dried sliced apples, ground into pulp or granules, to which an arsenical is added, magnesium arsenate being the most satisfactory. The bait is broadcast over the strawberry plants at the rate of about 70 pounds per acre.

Mote and Wilcox (57) tell about the bait method used in Oregon. They remark that a homemade bait consisting of 95 pounds of ground dried apple waste, mixed with 5 pounds of calcium arsenate, kills the strawberry-root weevils. A commercial bait is also reported to be efficient. .

Downes (13) further experimented with baits for strawberry-root weevils. He states that apple waste containing about 20 per cent of moisture was found more attractive than super-dried bait, and that sodium fluosilicate was the most suitable poison to use with apples containing that percentage of moisture. Two applications of the bait are recommended, the first in April and the second in June.

(c) BAITS FOR THE JAPANESE BEETLE

A study of the chemotaxis of the Japanese beetle was begun in 1922 at the Japanese Beetle Laboratory in New Jersey, and since that date several persons have worked on it, but some of them have never received credit in the published papers on this subject. This is particularly true of F. J. Brinley, who did the work in 1923 and discovered that geraniol was the most important attractant used. Richmond and the present writer continued the work in 1924, the former doing the field-work and the latter the laboratory work. Some of Richmond's results have been published, but since those of the writer were only preliminary they still remain unpublished.

The first authentic report on this subject is by Smith (76), who states that in chemotactic studies it has been found that Japanese beetles are strongly attracted by geraniol, and nearly 50,000 beetles in 1924 were collected from baits containing this substance. Bait mixtures, containing bran, molasses, and geraniol retain the odor for a long time if protected from the rain. Eugenol, citral, and citronellol as attractants, and tar oil as a repellent, appear to have some value.

Richmond (66) gives a detailed report on this subject and tells about the earliest experiments conducted. Since the beetles were known to have favored food plants and were strongly attracted to ripening fruit, various chemicals were tested in 1922 to ascertain if the fruit odors might be imitated. To determine whether beetles could be attracted to the sources of odors, a number of essential oils were sprayed on foliage. The results indicated that the oils of sassafras, hemlock, mustard, and lemon, and iso-amyl valerate were somewhat attractive. More detailed experiments were conducted in 1923 and a large number of compounds were studied. Bran-bait mixtures, put in cans which hung in trees, were used. Among the oils, sassafras and clove were easily the leaders, while ethyl alcohol, geraniol, and eugenol proved to be the most important constituents. In 1924 greater detailed studies were undertaken. The adult beetle was found exceedingly susceptible to the influence of color, odor, temperature, humidity, and light. The six leading chemicals tested are geraniol, eugenol, citronellal, citral, citronellol, and diphenyl ether. Geraniol proved to be far superior to the other five. In other experiments emulsions were tested. When cloths (1 foot square) were dipped in a 10 per cent emulsion of geraniol and suspended in orchards (pl. 1, A), beetles were drawn as if by a magnet and 13,000 beetles were collected on 12 cloths over a period of 5 successive days. In 1925 and 1926 this project was much expanded so that it included the testing of various types of bait cans and bait traps. The best type of trap devised was cylindrical in shape. A single one of these caught over 13,000 beetles in 8 hours. Richmond's summary follows:

Geraniol is clearly the primary attrahent of the Japanese beetle but its combination with eugenol materially lowers the cost and increases its effectiveness. During the summer of 1924 over 65,000 beetles were actually collected from the bait can experiments. Nearly 50,000 of these beetles were present on geraniol baits alone. The results of experimentation in 1925 and 1926 were in keeping with these remarks, but, inasmuch as more extensive tests were conducted, the number of beetles collected was proportionately greater. The activities of the adult varied with temperature, humidity and vapor pressure. Females are attracted approximately one-third more frequently than males when geraniol and most other chemicals are employed. Molasses has only a slight attractive

value. Satisfactory traps have been evolved and it seems possible that they will have considerable value in reducing the number of beetles in a given orchard. Bran retains odors over long periods if protected from the rain. Geraniol has been satisfactorily incorporated in poison sprays although its odor is not retained for a long enough period. To this end experiments on the absorption of this chemical on charcoal, clays, etc., are under way. The value of geraniol, when used in connection with a contact spray, has been demonstrated. Eugenol, citral, citronellol and citronellal follow geraniol as attractive agents.

It is further stated (3) that methods have been devised whereby geraniol may be used to concentrate the beetles in a relatively small area. It was found that by spraying less than an acre of orchard with geraniol, beetles could be drawn on the leeward side of the orchard for a distance of nearly one-half mile within the first 15 minutes after the spray had been applied. This makes it possible to destroy large numbers of beetles with a comparatively small quantity of a contact spray.   .

Van Leeuwen and others (87, 90) determined that acetic acid, an accumulation of beetles, geraniol, and fermented apple juice attract these beetles. It was discovered that the beetles would gorge themselves upon foliage sprayed with a mixture of lead arsenate and refined sugar, on trees to which they had been attracted by geraniol (pl. 1, B). More beetles fed on this foliage than on unsprayed leaves, and consequently the mortality was greater than ever before obtained. Smith (78) more recently reports that a combination of lead arsenate and refined cane-sugar sirup has been found useful as a spray on noneconomic plants. The beetles are strongly attracted to it and eat it readily. He says that this preparation is probably one of the most effective lethal sprays yet devised for the Japanese beetle. Owing to its tendency to injure foliage it is not recommended for use on economic plants.

Metzger (52) and Richmond and Metzger (68) describe various types of traps, one being called the standard bait trap. Each kilogram of the standard bait contains 500 grams of bran, 455 grams (350 cc.) of molasses (refiners' sirup 75 per cent), 44 grams (40 cc.) of glycerine, and a quantity of an attractant. With geraniol as the attractant making 5 per cent of the prepared bait, the bran-glycerine-molasses mixture does not deteriorate to any marked degree when exposed to the weather, and its attractive odor has been retained more than three years in some traps. In practice, baits were renewed twice a month, 150 grams of the prepared bait being put in each trap. The best bait, however, was found to be a technical geraniol, 58.8 per cent pure, used in the proportion of 2.5 per cent with eugenol in the proportion of 0.25 per cent of the total material. The total number of

beetles caught in 39 traps in 1926 was about 2,000,000, one trap catching 13,476 in one day. These traps were used also in connection with ecological investigations, and to obtain data on the degree of infestation at different points in different years. Beetles are caught in the traps before any are observed in the immediate neighborhood. As a result of these investigations various types of traps have been put on the market by commercial firms. In the 1929 report on the Japanese beetle, Smith (78) has the following to say about geraniol and traps:

Several years ago chemotropic investigations revealed that geraniol, one of the higher alcohols, was extremely attractive to the Japanese beetle. Few, if any, other insects have been found to be attracted to any degree by this chemical and it is apparently a specific for this insect. In commerce it is commonly used as an ingredient in the cheaper perfumes. Geraniol has been utilized in several ways in the control of the beetle; these include combining it with poisoned baits, as a means of concentrating the beetles in a small area where they may be killed with contact sprays, or more often as a constituent of baits used in mechanical traps. The Japanese beetle traps have come into wide use by residents in the suburban area around Philadelphia. In conjunction with spraying, the traps are useful in capturing large numbers of beetles. During the summer of 1929, 500 traps were placed on a 15-acre estate in the heavily infested district near Roxborough, Pennsylvania. The record of collections in these traps during the period between July 9 and August 23 gives a total of 1,874½ pounds of adult beetles and represents approximately 10,000,000 individuals. Many types of beetle traps are now on the market, ranging in price from 10 cents upward. The traps have not yet become sufficiently effective to warrant their use on farms. In fact, the presence of large numbers of traps may attract many beetles which are not captured, with the result that the grub population in the soil, in the vicinity of the traps, is greatly increased over what it would have been had the traps not been used.

During the past few years traps have come into general use for catching large numbers of Japanese beetles, but for various reasons a large percentage of the insects attracted to the traps are not caught; therefore, Mehrhof and Van Leeuwen (49) devised and perfected an electric trap (pl. 2) which not only attracts the beetles but kills practically all of them that come to it. This trap, in the form of a hollow cube, is 3 feet on each side, with parallel wires, ⅝ inch apart, on all four sides and on the top. The most effective bait was geraniol emulsion, sprayed on peach foliage which was suspended in the center of the trap. By this method beetles were at times attracted from a distance of one-fourth mile.

Siegler and Brown in 1927 (74) first published on the idea that attractive baits might be used advantageously in scouting for injurious insects. During the season of 1929 the Federal Plant Quaran-

tine and Control Administration made practical use of this idea by installing bait traps along the edges of the Japanese-beetle infested zones. So far little has been published on this particular phase of the work. According to the report of Secretary of Agriculture Hyde (27) the use of beetle traps at Baltimore and Washington, and in Alexandria County, Virginia, has resulted in the collection of great numbers of beetles. The possibility of substantial control at such isolated points by this method will thus be given. It has already been demonstrated that enormous quantities of beetles can be collected by trapping. In fact, on a single property in Pennsylvania (not New Jersey as reported) nearly a ton of beetles were thus collected in 1929. In the heavily infested areas, such trapping is of little value unless the employment of this method is general. Van Leeuwen (88) states that 25,000 of the Government standard traps, which he illustrates, were used by the Plant Quarantine and Control Administration during 1929 in its scouting work to determine the presence of beetles. Rex (65) illustrates and briefly discusses these traps and gives the bait formula recommended by the Japanese Beetle Laboratory in New Jersey. Van Leeuwen and Metzger (89) give the very latest information about traps for the Japanese beetle. They recommend the following formula for one baiting of a standard trap.

Geraniol (at least 58 per cent pure).............	15	grams (4 teaspoonfuls)
Eugenol (U. S. P.)...........................	1.5	grams ($\frac{1}{2}$ teaspoonful)
Bran	75	grams (1$\frac{1}{2}$ cups)
Water	13	cc. (1 tablespoonful)
Molasses	39	cc. (2$\frac{1}{2}$ tablespoonfuls)
Glycerine (C. P)....	6	cc. (1$\frac{1}{2}$ teaspoonfuls)

Figure 4 was drawn by the present writer and illustrates the various parts of one of the standard traps.

At this place a few more remarks concerning the attractiveness of geraniol should be made. The effort is usually made to correlate attractive odors either with the food or opposite sex of an animal; but in some cases it is questionable whether food, or sex, or some unknown factor, is involved. For example, why should the banana-like odor of amyl acetate attract grasshoppers, or certain beetles? And why does the odor from the catnip plant attract members of the cat family? In regard to the attractive power of geraniol, a food odor is probably involved, although we know little about it. Smith (76, p. 59) and Smith and Hadley (79, p. 58) in two of their earlier reports remark that several of the essential oils were found to be highly attractive to the Japanese beetle, and that on studying these oils, it was discovered that one of the higher alcohols, geraniol, was
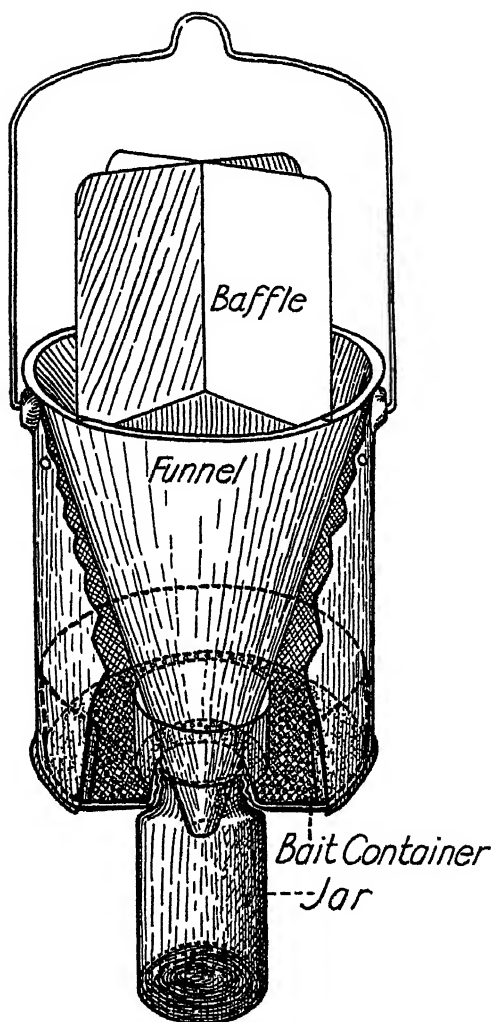
Fig. 4.—Japanese beetle trap, used by the Federal Plant Quarantine and Control Administration, showing parts of it in a cut-out perspective view. It is one-fourth natural size and was drawn by the writer by using a 1929 trap and a drawing of a 1930 trap, the latter being furnished by Mr. Courtney. The beetles, attracted by the odor from the bait in the bait container, fly directly into the funnel or strike the baffle and then fall down through the funnel into the fruit jar, where they cannot escape because they can neither fly out nor climb the walls of the jar.

a constituent of all the oils found to be distinctly attractive. Tests were made of a series of the preferred food plants, and in all cases these plants contained geraniol in varying quantities. The present writer has seen no report by a chemist concerning the last statement; but as regards fruit, Power and Chesnut (61) found geraniol in apples. They used only the parings of the McIntosh, one of the most fragrant varieties of apples, and say that geraniol, either in the free state or in the form of esters, is probably contained in varying quantities in all the numerous varieties of apples, although to the greatest extent in those which possess its distinctive odor. Power and Kleber (62) tell us that the two oils, one from sassafras bark and the other from sassafras leaves, are fundamentally different in regard to their chemical compositions. Oil from sassafras bark contains eugenol but no geraniol, while oil from sassafras leaves contains geraniol but no eugenol. There are also other differences. The fact that Japanese beetles were observed to be fond of sassafras leaves led to tests in which the oil of sassafras was used; after learning that oil from sassafras leaves contains geraniol it was only natural to continue using geraniol in bait mixtures.

A popular impression is that Japanese beetles are fond of geraniums and that our supply of geraniol comes from these plants, but this is far from the truth. Ballou (4) informs us that these beetles do feed upon the flowers and to a limited extent upon the foliage of cultivated geraniums (*Pelargonium* spp.), but with deleterious effects to themselves, because this food is toxic to them. Most of our commercial supply of geraniol is said to be derived from the oil of citronella, but in perfumery much of it also comes from the oil of palmarosa or Turkish geranium. Geraniol also occurs in the oils of lemon-grass, geranium, rose, sassafras leaves, and other essential oils.

<center>(D) BAITS FOR OTHER BEETLES</center>

Since 1916 it has been reported in numerous publications that certain sugarcane cockchafers in Australia can be attracted by odors from various chemicals and by the aromas distilled from their food plants, but it seems that so far no practical results have been obtained. Other reports by Jarvis (34, 36), however, indicate that poisoned baits have a practical value in helping to control the grubs of these beetles.

For years it has been known that poisoned-bran baits are of considerable value against the common May beetles and more recently Vickery and Wilson (92) used a bait consisting of 20 pounds of

wheat bran, 1 pound of Paris green, 1 quart of sirup, and the juice of 3 lemons or 1 teaspoonful of anise oil successfully against a wingless May beetle.

McKinney and Milam (48) and Gilmore and Milam (19) have successfully used a poisoned-bran bait against the grubs of the green June beetle in tobacco-plant beds and in a tobacco field.

A large white grub of a dynastid beetle is the most serious pest of sugarcane in St. Croix. The control recommended in 1916 by Smith (80) was a poisoned bait.

Poisoned-bran mash was the best control used by Cooley (10) in 1917 against the spinach carrion beetle.

Using a poisoned-bran bait in 1916 Scholl (71) destroyed the striped blister beetle on alfalfa and tomatoes.

Newman (59) in 1929 reports that a poisoned-bran bait gave excellent results against a subterranean clover weevil.

Jack (32) in 1928 reports that over 95 per cent of certain weevils in a maize field were killed by one application of a bait consisting of 1 pound of sodium arsenite, 8 pounds of sugar, and 10 gallons of water on chopped fodder.

During the seasons of 1926, 1927, and 1928, over 1,000 traps, containing fermenting sugar or molasses, were used in a peach orchard in Pennsylvania for the purpose of trapping oriental fruit moths. Frost and Dietrich (16) report that incidentally 40 families of beetles, including 188 genera and 258 species, were also caught in these traps.

Snapp and Swingle (81) have recently tested a large number of aromatics, including various steam distillates and other odorous materials derived from the food of peach insects. A large number of chemicals were found, under orchard conditions, to be slightly attractive to various peach insects, as well as to the plum curculio, but none showed much promise of being valuable from the standpoint of control.

Garman and Zappe (18) have also recently conducted many tests, trying to find attractants and repellents for the plum curculio. They remark that curculios are very sensitive to odors. Acetaldehyde and malic acid were the only substances used in the laboratory which showed much attractive power, but when these substances were tested in the field no curculios were trapped.

In conclusion under this heading a few remarks may be made about the present writer's (45) results obtained when testing potato beetles in an olfactometer. In this study no baits were actually used, but it was proved for the first time that plants (not flowers) attract insects

by emitting odors. Since odors from the steam distillates and emanations from 4 or 5 species belonging to the potato family attracted potato beetles, it was then suggested that the chemist tell us what constituent or constituents, common to these plants, did the attracting. If we had this information, we might be able to use these substances in poison baits.

(E) REPELLENTS USED AGAINST BEETLES

Under this heading many repulsive substances are regarded as repellents, but for some of them a more appropriate word would be deterrents; nevertheless, there is little distinction between these two words. Let us define a repellent as an odorous substance, which by means of its unpleasant exhalations repels insects before they have touched it; and a deterrent as an inodorous substance which repels insects after they have touched it. Thus defined, a deterrent repels mostly, if not entirely, through the sense of touch; while a repellent operates either through the sense of smell or, if its exhalations are poisonous, then through the breathing pores. These definitions are easily made, but it is perhaps almost impossible to have a deterrent which is totally inodorous to insects; and furthermore, other factors are often involved. These terms have been used loosely by various writers, and since this subject is yet confused, the present writer will still continue to use them without attempting to explain how the enumerated substances repel, deter, or otherwise keep insects away from plants. The following remarks by the writer's reviewers help to elucidate the subject.

In regard to the Japanese beetle, Doctor Van der Meulen and Mr. Van Leeuwen believe that there should be another subdivision of repellents to include those substances which mask attractive odors; for example, those from geraniol. We might call these " maskers " or " neutralizers," because they repel from a short distance merely by covering up or neutralizing the attractive odors. Relative to " inodorous " materials, Japanese beetles may also be repelled before touching dusted or sprayed food by means of the sense of sight. In regard to the repellency of the arsenates, the subject of toxicity should also be considered; but at present we are not able to evaluate the various factors, including the senses of sight, smell, touch, taste, and probably a general sense connected with the digestive system.

After reading the preceding definitions, Dr. F. L. Campbell proposed that attrahents, now usually called attractants, should be divided. The odor from geraniol causes the Japanese beetle to orient and to move toward this substance; therefore, geraniol is a true

attractant. In the course of random movements certain other insects may come upon sugar, for example, which holds them after they have touched it. In this case, Campbell says that sugar might be called a true " arrestant." If insects have true senses of smell and taste, an attractant then attracts through the sense of smell and an arrestant arrests through the sense of taste.

Since entomologists already know much of the following information, only the more important references consulted will be cited here. The substances inodorous or slightly odorous to us, which have been found repulsive to insects, may be briefly discussed as deterrents. Whitewash may be considered the first deterrent used. Whitewashing the bases of fruit trees has been practiced for years. It is still questionable whether such a practice is of any real economic importance, but its advocates claim that the lime in it has a tendency to drive away noxious insects and may be slightly injurious to insect eggs. The most improved and best mixture of whitewash, as recently recommended in France, consists of lime, calcium arsenate, lime sulphur, and water. In this case the lime might act as a deterrent and the lime sulphur, which has a strong disagreeable odor, as a repellent. One of the most efficient deterrents used in the United States is air-slaked lime, which is employed extensively for dusting melons and cucumbers to prevent the attacks of the striped cucumber beetle. It is also said to prevent injury to stored beans by the bean weevil. In Germany a mixture of white sand and hydrated lime has recently been used to deter flea-beetles. Paints, particularly white-lead paint, are recommended for preventing boring beetles from entering wounds on fruit trees. The coat of paint covering the fresh wound preserves the wood and also acts as a mechanical barrier to the beetles. Lead arsenate, when sprayed or dusted on foliage, deters a number of insects, including the Japanese beetle, western cabbage flea-beetle, desert corn flea-beetle, and striped cucumber beetle. Most of the arsenicals deter the Mexican bean beetle. Bordeaux mixture sprayed on the leaves of eggplant and potatoes deters flea-beetles and the potato leafhopper, which causes the disease called " hopperburn."

In regard to repellents used against beetles, the first ones used were probably decoctions of certain poisonous plants. As early as 1848 leather waste from tanneries, when put among plants in Germany, was found to be a repellent against flea-beetles, and more recently in France sawdust coated with coal tar when placed among the plants repelled these insects. The most successful repellent used against these tiny insects and the striped cucumber beetle in the United States

is nicotine dust. Since it is almost impossible to kill flea-beetles by using arsenicals or other insecticides, the repellent method is an important control measure.

In Europe there has been considerable experimenting with repellents to keep beetle larvae, particularly white grubs, from attacking the roots of plants. The odorous substances were usually worked into the soil around the bases of the plants, but it is doubtful whether much protection ever resulted. In France and Belgium crude naphthalene mixed with sand was used. In France three other repellents were found more or less effective—first, residue of glue; second, naphthalene and kerosene mixed with sawdust; and third, crude oil mixed with lime, plaster of Paris, and feces. In Germany sulphur was worked into the ground around strawberry plants. In England naphthalene was successfully used against wireworms in gardens, and in Australia crude naphthalene was effective against wireworms injuring sugarcane.

McColloch and Hayes (40) have recently reviewed the methods and enumerated the repellents used to protect germinating seeds and roots and to prevent the invasion of the soil by underground insects, particularly beetles. Numerous substances have been recommended as repellents, including crude carbolic acid, turpentine, naphthalene, paradichlorobenzene, creosote, coal tar, oils of lemon and tansy, kerosene, and phenol. They state that no satisfactory repellent has yet been found which can be depended upon under varying conditions existing in the soil. They believe that this subject needs further investigation.

Since the Japanese beetle is fond of ripening fruit, particularly apples and peaches, and since it is not advisable to spray early fruit with arsenicals, ripening fruit should be protected by other means. Therefore, much experimental work has been done to develop an effective repellent to take the place of the arsenicals. Metzger and Grant (54) have developed smudge candles, which, when lighted and hung in peach trees, give off ill-smelling smoke for a period of five to eight hours. The mixture, to be burned slowly without producing a flame, was put in a wire-screen cylinder, 31 inches long and 2.25 inches in diameter. In conclusion they say that wood flour and potassium nitrate, when properly mixed, form a satisfactory base for smudges. The fumes from pine-tar oil, Dippel's oil (bone oil), and a commercial mixture of chloronaphthalenes, when given off from burning smudge candles, are definitely repellent to Japanese beetles. Air currents in the orchard, however, prevented the repellent smoke from giving satisfactory control of beetles on early peach trees.

Metzger (53) describes five methods used in testing 430 materials, alone and in combination, as repellents for the Japanese beetle. Under method 1, "testing material in comparison with a known attrahent," 306 materials were tested, and 45 of them decreased the attraction of the geraniol-eugenol combination. Beginning with the one most repellent, the first ten in the list are o-cresol, pine-tar oil, phenol, Dippel's oil, high boiling tar acids, coal-tar neutral hydrocarbon oil, trichlorobenzene, crude dichlorobenzene No. 1, alpha chloronaphthalene, and crude dichlorobenzene No. 2.

Another difficult test has been to find a successful repellent for wood-boring beetles. The first object is to prevent them from entering the living trees, lumber, or manufactured wooden articles, and the second object is to kill them or drive them out of their burrows after they have once entered. Little success has yet been accomplished along this line, but it is easier to prevent their entrance than to control them later. In Brazil a mixture consisting of crude carbolineum 1 part, quicklime 10 parts, and water 40 parts is painted on the trunks of citrus trees to prevent the entrance of borers. In the United States carbolineum and creosote are often applied to the trunks of aspen trees in forests to prevent the entrance of the aspen borer. A successful repellent has recently been recommended by Pettit (60) against flat-headed borers which do considerable damage to apple trees. Following a special procedure a thick solution is prepared by using 50 pounds of laundry soap, 3 gallons of water, 25 pounds of flake naphthalene, and 2 pounds of flour. After warming and thinning this mixture to the consistency of heavy cream, it is applied several times with a brush to the trees.

The Lyctus powder-post beetles, which cause much damage to hardwood lumber, implement handles, furniture, etc., throughout the world, may be deterred and repelled by several substances. In the United States, according to Snyder (82), the usual method recommended is to immerse the lumber, already infested or liable to infestation with these borers, in vats of kerosene, or in a mixture of creosote and kerosene, or in one of creosote and naphtha. The writer has recently been told that these beetles may be repelled by using coal-tar creosote and orthodichlorobenzene. The lumber and handles which can not be treated by the vat method may be stored in closed sheds and close-fitting houses and then sprayed at intervals with these chemicals. In Great Britain lumber stacked in the open is often treated with cold paraffin mixed in equal parts with oil of cedar, linseed oil, or a heavy mineral oil. To lumber stored in sheds orthodichlorobenzene is applied with a brush or sprayer, or paradichlo-

robenzene is scattered on top of the stacks and suspended in bags from the roofs of the sheds.

Carpet beetles, also called "buffalo moths," often do considerable damage to carpets, woolens, furs, feathers, and upholstered furniture. One of the control measures is to prevent them from coming in contact with these articles by using repellents, such as naphthalene in the form of flakes and moth balls, paradichlorobenzene, or camphor, or by the use of red cedar chests.

2. ORIGINAL WORK ON MEXICAN BEAN BEETLE

In 1928, Mr. J. E. Graf, Assistant Chief of the Bureau of Entomology, handed the writer a manuscript entitled "Some chemotropic responses of the Mexican bean beetle," by Wallace Colman, who tested over 200 materials, but found only a few to be attractive while a larger number were repellent. According to the results in this unpublished manuscript, which deals with the sense of smell alone, the following seemed to be attractive: banana peel, amyl acetate, vanillin, coumarin, corn sirup, honey, and molasses of the higher grades; while certain lead and arsenic compounds, including lead arsenate, seemed to be repellent. Using different methods the present writer tested all of the above supposed attractants, but found only the corn sirup and molasses to be attractive, while lead arsenate proved to be repellent.

(A) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING AN OLFACTOMETER

Using the writer's (45) olfactometer, with the plant chamber disconnected, no important results were obtained, but the following remarks may have some theoretical interest. On several occasions fresh bean leaves were put in the small bottle, used for holding the odorous substance to be tested. In each test in which only a few leaves were used the odor or exhalation from the leaves was attractive to the bean beetles, although the highest attraction was only 57.9 per cent. In two other tests the bottle was filled full of leaves. The results (61.8 per cent and 72.5 per cent), instead of showing attraction, showed repulsion, indicating that attractants when concentrated become repellents. The odors from table molasses (1 part molasses and 1 part water) and the water extract (diluted juice) of bean leaves were also found to be slightly attractive.

The following, used in minute quantities, were repellent: oil of peppermint, creosotum, nicotine sulphate, banana peel, amyl acetate, and geraniol.

(B) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING FEEDING METHOD

A search for attractants and repellents was begun in 1928, but during that year no important results were obtained. The following remarks, however, may be of some interest. A liquid, highly scented with skatol, when sprayed on bean foliage in the laboratory did not delay the eating of the leaves. A piece of cotton, scented with oil of peppermint, was put among some bean leaves. The leaves were eaten as usual. Four odorous powders were prepared with the aid of heat by using (1) nicotine sulphate and lead arsenate; (2) nicotine sulphate and lime; (3) tar and lead arsenate; and (4) tar and lime. When these powders were mixed with soap solution and sprayed on bean foliage in the laboratory the sprayed leaves were eaten almost as readily as were the untreated leaves nearby.

A wire-screen cage, 4 feet long, 3 feet wide, and 3 feet tall, containing hundreds of adult beetles, was put in the insectary. A pan containing bran bait was suspended in each corner. The first bait was flavored with black-strap molasses; the second, with amyl acetate; the third, with vanillin; and the fourth contained only bran and water. The second and third baits each attracted only a few beetles; the fourth, many; while the first, more than twice as many as the fourth. It thus seems that the molasses bait was slightly attractive.

The preceding test was repeated by putting a pan containing black-strap molasses and water in each corner, an aromatic being put in each of three pans. The pans containing coumarin and vanillin attracted practically the same number of beetles; the pan containing amyl acetate, several more; and the pan containing only molasses and water, a few more, but the attraction was not significant.

The foregoing test was repeated by putting three pans in the cage. One contained the juice from bean leaves; the second, the remaining pulp of the leaves and diluted table molasses; and the third, diluted table molasses. The first and third attracted beetles in equal number, while the second attracted three times as many, not a sufficient number to appear significant.

A pan containing fermenting table molasses was next put in the center of the cage. For five days the beetles in it were counted, but no striking attraction was noticed at any time.

Not yet having found any substance which seemed promising as an attractant, the writer in 1929 decided to test a large number of materials. After spending much time, 104 aromatic chemicals, 3 brands of molasses, 2 varieties of canesugar, and 1 highly scented honey were tested. The method consisted of testing 8 substances at one time in a small wire-screen cage. This method was found to be

3

faulty, yet the writer believes that if a strong attractant in the proper concentration had been used striking results could have been obtained quickly. No important results were really obtained, but the following remarks may be worth recording. Using water as a control, methyl anthranilate, benzaldehyde, methyl benzoate, terpinyl acetate, dibenzyl ether, tertiary amyl alcohol, and ethyl iso-valerate seemed to be more or less attractive, but not sufficiently so to be significant. The most promising chemical, methyl anthranilate, was tried in the bean patch but attracted no beetles. In the preliminary tests while using water and portions of bean leaves as controls, a good grade of table molasses diluted with water was nearly always preferred to the controls. Fermenting table molasses was attractive up to the vinegar stage of fermentation, after that its attractiveness ceased. During warm weather when the beetles were thirsty, a long series of tests was conducted to ascertain their preferences when given water, molasses, sugar, and honey. The final results showed their preferences to be: (1) water alone; (2) corn sirup and granulated sugar, practically the same; (3) table molasses and sugar sirup, the same; (4) brown sugar; (5) honey; and (6) black-strap molasses. The sugar sirup consisted of boiled brown sugar and water (about 1 to 1). The brown sugar was a saturated solution. Each of the others was half sweet substance and half water. On August 5 and 12, pans containing table molasses, corn sirup, and black-strap molasses were put between rows of beans in the garden. Observations were taken thereafter for several days, but not a bean beetle was seen in the pans, although many moths and certain other insects were caught in the baits.

(c) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING AN IMPROVED
FEEDING METHOD

In order to obtain comparative results which could be treated statistically, four cages were constructed. Each cage was 8.75 inches square, 0.75 inch deep (inside dimensions), and had a wooden bottom and a top of wire-screen and glass (fig. 5, A). The substances to be tested were put on pieces of cardboard (W, X, Y, and Z), 1.75 inches square, which were arranged in a row, being equally spaced between themselves and the sides of the cage. From left to right the positions of the cardboard were numbered 1, 2, 3, and 4. In the first series of tests the substances were arranged in the four cages as indicated by the first row in the four diagrams (B, C, D, and E); in the second series, as indicated by the second row; in the third series, as indicated by the third row; and in the fourth series, as

indicated by the fourth row. According to this arrangement of food, no two rows in the same cage were exactly alike; likewise, no two rows of all 16 rows were identical, although the distribution of food was not so complete. These four series of tests were conducted during the forenoon, and then usually repeated in the afternoon. Each

B

W	1st Series X	Y	Z
X	2d W	Series Z	Y
Y	3d Z	Series W	X
Z	4th Y	Series X	W

C

Y	1st W	Series Z	X
W	2d Y	Series X	Z
Z	3d X	Series Y	W
X	4th Z	Series W	Y

D
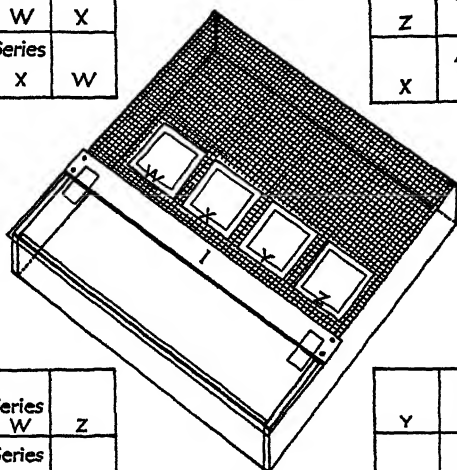
X	1st Y	Series W	Z
Y	2d X	Series Z	W
Z	3d W	Series Y	X
W	4th Z	Series X	Y

E

Y	1st Z	Series X	W
Z	2d X	Series W	Y
W	3d Y	Series Z	X
X	4th W	Series Y	Z

Fig. 5.—Diagrams of wire-screen cage (A) and arrangement of substances (B, C, D, and E) to be tested by bean beetles. See text, p. 32, for further explanation.

individual substance used was therefore tested 16 times in the forenoon and usually 16 times in the afternoon.

It was difficult to decide whether tests of this kind should be conducted in the dark-room or in the well-lighted laboratory. After trying the dark-room it was observed that the bean beetles did not eat freely either in artificial light or in total darkness. So it was decided to place the cages on a table by a south window, but not in the

direct sunshine. As suspected under these conditions, the number of beetles counted in the four positions varied greatly. More beetles were always counted in the outer positions (Nos. 1 and 4) than in the inner ones (Nos. 3 and 4). This was caused largely by the beetles following the sides of the cage while moving toward the window. In 40 series of tests, selected at random, 67.04 per cent of the beetles were counted in the outer positions and 32.96 per cent in the inner positions. The following percentages were counted in the four positions: 37.06 per cent in position 1; 17.01 per cent in position 2; 15.95 per cent in position 3; and 29.98 per cent in position 4. Since each substance used lay in all four positions during any one series of tests, these large differences did not supposedly change the arithmetic mean, but they greatly affected the probable error, because each number of beetles counted on a substance was considered a statistical item. Since the beetles ate more freely during the forenoon than during the afternoon, the probable errors were further affected.

In addition to the preceding statements, the general plan in conducting these tests was to put 60 beetles of approximately the same age and physiological condition in each cage. The number of beetles on (or touching) the food was counted at intervals of 45 minutes, and this number was considered a statistical item. The food was renewed whenever necessary to keep it in an appetizing condition, and to prevent contamination it was usually put on unused pieces of cardboard. Since the beetles had a tendency to congregate at the ends of the cages nearest the window, the cages were often turned end for end, thus causing the insects to scatter more evenly. The daily temperature and relative humidity in the laboratory were recorded, and a record of the outside climatic conditions was also kept. In brief, everything possible was done to obtain reliable data which could be treated statistically. The arithmetic mean and probable error are stated in tables 2 to 11 for reference in connection with the following discussion. Since the statistical items were never less than 16, the following formula for calculating the probable error was used—

$$P.E.\, m = \pm 0.6745 \frac{\sigma}{\sqrt{N}}$$

(1) *Beetles can distinguish differences between water and salty liquids.*—To determine whether Mexican bean beetles " like " or " dislike " the four classes of substances which produce the four human attributes of taste, many series of tests were conducted. The results obtained are given in tables 2 to 5.

To ascertain whether these insects " like " salty water, sodium chloride, potassium nitrate, and magnesium sulphate (epsom salts)

TABLE 2.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and salty liquids*

Methods of feeding salty liquids	Total number of beetles on cotton	Mean and probable error	Relative value of beetles on cotton	Number of set of beetles	Date	Number of tests
Water on cotton (control)	106	3.31 ± 0.44	1.00			
Sodium chloride on cotton	13	0.41 ± 0.12	0.12	16	Aug. 29-30	32
Potassium nitrate on cotton	30	0.94 ± 0.28	0.28			
Magnesium sulphate on cotton	56	1.75 ± 0.27	0.53			

TABLE 3.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and sour liquids*

Methods of feeding sour liquids	Total number of beetles on cotton	Mean and probable error	Relative value of beetles on cotton	Number of set of beetles	Date	Number of tests
Water on cotton (control)	150	9.38 ± 1.12	1.00			
Acetic acid on cotton.	36	2.25 ± 0.61	0.24	16	Aug. 31	16
Hydrochloric acid on cotton	31	1.94 ± 0.47	0.21			
Lemon juice on cotton.	27	1.69 ± 0.44	0.18			

TABLE 4.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and bitter liquids*

Methods of feeding bitter liquids	Total number of beetles on cotton or leaves	Mean and probable error	Relative value of beetles on cotton or leaves	Number of set of beetles	Date	Number of tests
Water on cotton (control)	171	10.69 ± 0.84	1.00			
Strychnine on cotton.	102	6.38 ± 0.78	0.60	14	Aug. 16	16
Quinine on cotton....	83	5.19 ± 0.72	0.49			
Picric acid on cotton.	46	2.88 ± 0.26	0.27			
Leaves, sprayed with water (control) ..	198	6.19 ± 0.29	1.00	20	Sept. 14	32
Leaves, sprayed with beetle extract	172	5.38 ± 0.39	0.87			

were used at the rate of 1 gm. of salt to 25 cc. of water (table 2). Pieces of cotton of equal size were wet with tap water and with the three salty solutions, and then they were put on the pieces of cardboard, as already described.

(2) *Beetles can distinguish differences between water and sour liquids.*—To ascertain whether the above statement is true, three

TABLE 5.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and sweet substances*

Methods of feeding sweet substances	Total number of beetles on cotton or leaves	Mean and probable error	Relative value of beetles on cotton or leaves	Number of set of beetles	Date	Number of tests
Water on cotton (control)	34	1.06 ± 0.23	1.00			
Cane sugar on cotton..	307	9.60 ± 0.75	9.03	16	Aug. 29-30	32
Grape sugar on cotton.	87	2.72 ± 0.35	2.56			
Saccharine on cotton..	15	0.47 ± 0.12	0.44			
Leaves, sprayed with water (control)	141	4.41 ± 0.36	1.00			
Leaves, sprayed with cane sugar	254	7.94 ± 0.41	1.80	20	Sept. 13	32
Leaves, sprayed with grape sugar	202	6.31 ± 0.44	1.43			
Leaves, sprayed with saccharine	113	3.53 ± 0.27	0.80			
Leaves, sprayed with water (control) ...	108	3.38 ± 0.33	1.00			
Leaves, sprayed with table molasses	261	8.16 ± 0.51	2.42	21	Sept. 16	32
Leaves, sprayed with corn sirup	174	5.44 ± 0.40	1.61			
Leaves, sprayed with black-strap molasses.	203	6.34 ± 0.41	1.88			

sour liquids were used, each of two being prepared at the rate of $\frac{1}{2}$ cc. of glacial acetic acid (99.5 per cent) or hydrochloric acid (85.9 per cent) to 25 cc. of water, and the third at the rate of 4 cc. of lemon juice to 21 cc. of water (table 3).

(3) *Beetles can distinguish differences between water and bitter liquids.*—To determine whether the above statement is correct, four bitter liquids were used, each of three being prepared at the rate of

50 mg. of picric acid, quinine sulphate, or strychnine sulphate to 25 cc. of water. The fourth was prepared by adding 25 cc. of water to the macerated bodies of 20 live bean beetles. The resulting liquid, when filtered, was yellowish and to the writer had a bitter taste and an unpleasant odor. It was sprayed upon bean leaves, which when dry were cut into pieces, one inch square, then put on the pieces of cardboard, and finally fed to the beetles (table 4).

TABLE 6.—*Tests to determine whether bean foliage sprayed with sweetened arsenicals is more attractive to Mexican bean beetles than unsprayed foliage*

Leaves: un-sprayed and sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control)..	74	2.31 ± 0.35	1.00			
Calcium arsenate and sugar	106	3.31 ± 0.31	1.43			
Magnesium arsenate and sugar	131	4.10 ± 0.33	1.77	18	Sept. 5	32
Lead arsenate and sugar	132	4.12 ± 0.30	1.78			
Unsprayed (control)..	131	4.10 ± 0.38	1.00			
Magnesium arsenate and table molasses..	194	6.06 ± 0.40	1.48			
Magnesium arsenate and corn sirup......	157	4.90 ± 0.49	1.20	22	Sept. 25	32
Magnesium arsenate and black-strap molasses	113	3.53 ± 0.40	0.86			

(4) *Beetles can distinguish differences between water and sweet liquids.*—To determine whether the above is correct, 24 series of tests were conducted by using six sweet solutions, each of five of them being prepared at the rate of 1 gm. or 1 cc. of granulated cane sugar, grape sugar (dextrose), a high quality table molasses, corn sirup, or black-strap molasses to 25 cc. of water; and the sixth at the rate of 20 mg. of saccharine to 25 cc. of water (table 5).

From the information given in tables 2 to 5, with additional notes, it may be concluded that Mexican bean beetles exhibit " likes " and " dislikes " when fed substances which produce the four human at-

tributes of taste. They "disliked" water containing salts, acids, bitter materials, and saccharine, but "liked" the other sweet substances, including cane sugar, grape sugar, table molasses, corn sirup, and black-strap molasses, and even showed preference between them. To the writer the saccharine solution was sweetest, but distasteful; the cane sugar, less sweet, and tasteful; and the grape sugar, least sweet, and less tasteful. The beetles showed "dislikes" and

TABLE 7.—*Tests to determine whether bean foliage sprayed with arsenicals, is repellent to Mexican bean beetles*

Leaves; unsprayed, and sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control) .	191	5.97 ± 0.49	1.00			
Calcium arsenate	160	5.00 ± 0.62	0.84	17	Sept. 3	32
Magnesium arsenate..	177	5.53 ± 0.56	0.93			
Lead arsenate	111	3.47 ± 0.40	0.58			
Unsprayed (control)..	275	8.59 ± 0.67	1.00			
Calcium arsenate	177	5.53 ± 0.50	0.64	17	Sept. 4	32
Magnesium arsenate..	122	3.81 ± 0.42	0.44			
Lead arsenate	122	3.81 ± 0.48	0.44			
Unsprayed (control)..	172	5.38 ± 0.46	1.00			
Calcium arsenate	159	4.97 ± 0.35	0.92	24	Sept. 27	32
Magnesium arsenate..	104	3.25 ± 0.25	0.60			
Lead arsenate	101	3.16 ± 0.22	0.59			
SUMMARY of above: Leaves, unsprayed (controls)	638	6.64 ± 0.33	1.00			
Calcium arsenate	496	5.17 ± 0.29	0.78	....	....	above 96
Magnesium arsenate..	403	4.20 ± 0.26	0.63			
Lead arsenate	334	3.48 ± 0.22	0.52			

"likes" in somewhat the same order. To the writer the picric-acid solution was most bitter, the quinine less bitter, and the strychnine least bitter. The insects "disliked" these solutions in about the same order. To the writer the solutions containing acetic acid and hydrochloric acid had practically the same degree of sourness, while the diluted lemon juice was sourer. The beetles also showed only slight differences between them. In regard to the salty solutions, the writer disliked only the magnesium sulphate solution, but the beetles preferred it to the other two.

(5) *Bean foliage sprayed with sweetened arsenicals is more attractive than unsprayed foliage.*—To ascertain whether the above is correct, 16 series of tests were conducted. The arsenicals were prepared as stated on the following page, then 1 gm. of granulated cane

TABLE 8.—*Tests to determine whether bean foliage sprayed with sweetened magnesium arsenate is more attractive to Mexican bean beetles than foliage sprayed with non-sweetened magnesium arsenate*

Leaves sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Magnesium arsenate (control)	71	2.22 ± 0.26	1.00			
Magnesium arsenate and table molasses (2 to 50)..........	192	6.00 ± 0.61	2.70			
Magnesium arsenate and corn sirup (2 to 50)	114	3.56 ± 0.39	1.60	23	Sept. 26	32
Magnesium aresnate and black-strap molasses (2 to 50)....	122	3.81 ± 0.43	1.72			
Magnesium arsenate (control)	82	2.56 ± 0.28	1.00			
Magnesium arsenate and black-strap molases (2 to 50)....	132	4.12 ± 0.36	1.61			
Magnesium arsenate and black-strap molasses (1 to 50)....	115	3.59 ± 0.29	1.40	25	Sept. 30	32
Magnesium arsenate and black-strap molasses (½ to 50)....	134	4.19 ± 0.32	1.63			

sugar or 1 cc. of a high quality table molasses, corn sirup, and black-strap molasses was added to 25 cc. of the spray mixture (table 6).

According to the results given in table 6, it is again shown that these beetles like their food sweetened.

(6) *Bean foliage sprayed with arsenicals is repellent.*—To determine whether bean foliage sprayed with arsenicals is eaten as readily as are unsprayed bean leaves, 24 series of tests were conducted. The

leaves were sprayed with calcium arsenate, magnesium arsenate, and lead arsenate at the rate of 1 pound of powder to 50 gallons of water. The calcium-arsenate mixture also contained lime at the rate of 1.5 pounds to 50 gallons of water (table 7).

The results given in table 7 clearly show that arsenicals are repellent, but not sufficiently so to prevent the foliage from being eaten. Lead arsenate was most repellent, magnesium arsenate was less so, and calcium arsenate was least repellent. The word " deterrent " is probably the better expression in this case.

TABLE 9.—*Tests to determine whether water extract and steam distillate of bean leaves are attractive to Mexican bean beetles*

Methods of feeding leaves and liquids	Total number of beetles on leaves or cotton	Mean and probable error	Relative value of beetles on leaves or cotton	Number of set of beetles	Date	Number of tests
Leaves, unsprayed (control)	190	5.94 ± 0.39	1.00			
Water on cotton....	28	0.87 ± 0.14	0.15			
Water extract on cotton	167	5.22 ± 0.40	0.88	21	Sept. 18	32
Water extract and cane sugar (1 to 25) on cotton.....	677	21.16 ± 0.82	3.56			
Water on cotton (control)	415	6.48 ± 0.41	1.00	21	Sept. 19	64
Distillate on cotton..	436	6.81 ± 0.43	1.05			

(7) *Bean foliage sprayed with sweetened magnesium arsenate is more attractive than foliage sprayed with non-sweetened magnesium arsenate.*—To determine whether the above is true 16 series of tests were conducted by using magnesium arsenate (1 pound to 50 gallons water) with molasses added at the rate of 2, 1, and ½ gallons to 50 gallons of the spray mixture (table 8).

The results given in table 8 once more show that sweetened food is preferred to non-sweetened food.

On September 30 four small bean plants, each bearing six leaves, were sprayed. Two of these were sprayed with magnesium arsenate alone and the other two with a mixture of magnesium arsenate and black-strap molasses (1 to 50). One plant sprayed with the non-sweetened mixture and one with the sweetened mixture were put to-

gether in one end of a cage, and the other two sprayed plants were arranged likewise at the other end of the cage. Soon after placing 100 beetles in the cage the insects climbed upon the sprayed foliage, paying apparently no more " attention " to the sweetened leaves than to the non-sweetened ones, but after a few hours and thereafter until October 3, when the experiment was ended, the sweetened leaves bore the more beetles and were the more eaten. The final result

TABLE 10.—*Tests to determine whether chemotaxis or phototaxis is more important in the finding of food by Mexican bean beetles*

Methods of feeding lerves and liquids	Total number of beetles on leaves or cotton	Mean and probable error	Relative value of beetles on leaves or cot ton	Number of set of beetles	Date	Number of tests and remarks
Bean leaves, not sprayed (control).	68	2.12 ± 0.31	1.00			
Apple leaves not sprayed	4	0 12 ± 0.02	0.06	22	Sept. 23	32 tests. Beetles in direct sunshine.
Green water on cotton	196	6.12 ± 0.76	2.88			
Green sugar water (1 to 25) on cotton..	635	19.84 ± 0.99	9.34			
Bean leaves, not sprayed (control).	116	3.62 ± 0.24	1.00			
Mulberry leaves not sprayed	19	0.59 ± 0.11	0.16			
Mulberry leaves, sprayed with sugar water (1 to 25)...	73	2.28 ± 0.30	0.63	22	Sept. 24	32
Bean leaves, sprayed with sugar water (1 to 25).........	221	6.91 ± 0.42	1.90			

showed that the sweetened leaves bore 69.7 per cent of all the beetles counted on the four sprayed plants.

(8) *Water extract and steam distillate of bean leaves tested.*—To test the diluted juice of bean foliage, a water extract was prepared by adding 50 cc. of water to 10 gm. of leaves, cut into small pieces. After macerating the pieces and decanting the liquid through cheesecloth, 50 cc. of a greenish liquid was secured. To test the steam distillate of bean foliage, 100 cc. of water was added to 30 gm. of leaves, cut into small pieces, and then 50 cc. of a clear and odorous distillate was collected (table 9).

The results given in table 9 show that when water extract of bean leaves was compared to unsprayed leaves it was about equally attractive, while sweetened water extract was about 3.56 times as attractive. Steam distillate from bean leaves was not attractive, but gave practically the same result as did water, indicating that its faint odor had no attractive influence.

(9) *Chemotaxis more important than phototaxis in the finding of food*. Sixteen series of tests were conducted to ascertain whether phototaxis or chemotaxis, or possibly thigmotaxis, is the more important in the finding of food. Squares of bean leaves, apple leaves,

TABLE 11.—*Tests to determine whether repellents would protect beans from the Mexican bean beetle*

Leaves: un-sprayed and sprayed with:	Total number of beetles on leaves	Mean and prob able error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control)..	226	7.06 ± 0.49	1.00			
Tar and lime........	216	6.75 ± 0.53	0.96			
Nicotine sulphate and lime	196	6.12 ± 0.47	0.87	19	Sept. 9	32
Derris product	120	3.75 ± 0.47	0.53			
Unsprayed (control)..	256	8.00 ± 0.64	1.00			
Cresol	251	7.84 ± 0.49	0.98			
Nicotine sulphate	219	6.84 ± 0.56	0.85	19	Sept. 10	32
Beta naphthol	142	4.44 ± 0.47	0 55			

and mulberry leaves, all of the same shape and size (1 in. square), but some bearing a film of cane sugar, represented practically the same color, form, and texture, but differed chemotactically. Cotton wet with green water and with green sugar water (a green dye being used) also somewhat resembled the leaves in color but differed in other respects (table 10).

The results given in table 10 show that sweetened food is preferred to non-sweetened food and that chemotaxis is more important than phototaxis in bringing about the results obtained.

(10) *Repellents would probably not protect beans*.—To ascertain whether certain substances, usually known as repellents, would keep the beetles away from the treated leaves in the four small cages, bean foliage was sprayed with the following: Tar and lime, combined as a dust; nicotine sulphate and lime, combined as a dust, a com-

mercial Derris product, consisting mostly of pyridine; cresol, U. S.P. (1 cc. shaken in 400 cc. water); 40 per cent nicotine sulphate in water (1 to 400); and beta naphthol (1 gm. powder in 400 cc. water; powder not all in suspension) (table 11).

The results given in table 11 show that the repellents more or less protected the leaves, but not sufficiently so to prevent them from being eaten. The Derris product and beta naphthol were the only ones which might be considered promising, yet their protective value was about equal to that of lead arsenate, as already shown in table 7.

III. THERMOTAXIS

After having searched the literature for references on other tropisms not yet discussed, the writer found a few more concerning Coleoptera, but only two of these references pertain to the orientation of beetles to temperature. Much experimental work on various temperatures, particularly as control measures, has been done, but very little of it can be discussed from the tropic point of view.

1. REVIEW OF LITERATURE

Fulton (17) devised a crude temperature gradient with which he determined that the choice of temperature of adult click beetles is much below the usual maximum temperature in open fields during summer. He also says that negative phototaxis causes the beetles to seek dark hiding places during the day. Wireworms, or the larvae of these beetles, were found more resistant to heat than were the adults, but they did not voluntarily seek higher temperatures. Seasonal movements of the larvae may be closely correlated with changes in soil temperature.

Grossman (21) tried three methods to determine the orientation of cotton boll weevils to heat stimuli, but decided that only the results obtained by using a new apparatus were reliable. This apparatus was constructed by using 16 copper bars $\frac{1}{8}$ inch wide and $\frac{1}{16}$ inch thick, with $\frac{1}{64}$ inch insulating space between each two bars. Using only two variables, temperature and light, 126 boll weevils were tested 1,993 times. The average temperatures to which they reacted definitely were 130° F. at the hot end of the apparatus and 26° F. at the cold end.

B. SENSORY RECEPTORS

Since tropic responses are brought about largely by external stimuli affecting either the special sense organs or others not definitely known and localized, called the general sense organs, it is only natural to discuss the tropic responses and sensory receptors in the same paper.

I. PHOTORECEPTORS

According to the phototactic responses of the Mexican bean beetle and its larva, already discused, the compound eyes and ocelli in this species are normally developed and seem to function adequately, so far as beetles are concerned. It is recalled that the adults are always photopositive and that the larvae up to the time of pupation are photo-positive, too, but when ready to pupate they become photonegative. Whether the negative reaction is caused by a change in the structure of the ocelli is not known.

Since the morphology of insects eyes has often been discussed and as the writer (46, 47) has recently cited reviews on this subject, no further discussion is needed here. Also, the other sense organs and senses of beetles will be discussed only briefly.

II. CHEMORECEPTORS

Chemoreceptors include both olfactory and gustatory organs, but we are not absolutely sure that insects have true chemoreceptors, al-though their organs certainly belong to the same category.

1. SO-CALLED OLFACTORY ORGANS

(A) ANTENNAL ORGANS

The organs on the antennae of the Mexican bean beetle are com-paratively few; that is, these antennae are nearly bare in comparison to most antennae (fig. 6). Only four types of sense organs were found on them. They are as follows: (1) Two groups of tiny hairs (*St*); and (2) three or four pores (*P*), called olfactory by the writer, lie on the base of the first antennal segment; (3) the Johnston organ (*J*) lies at the distal end of the second segment; and (4) five areas of thin-walled hairs (*OHr*) were found on the distal ends of the ninth, tenth, and eleventh segments. All of these structures are sense organs, because sense cells were found connected with them, while the larger hairs (*Hr*), usually called sense bristles, were found to be non-innervated.

Of these four types of sense organs only the olfactory pores and thin-walled hairs may be regarded as so-called olfactory organs. The thin-walled hairs are numerous and most of them lie on the dorsal surface of the antennae (fig. 6, *OHr*). Under a high-power lens they appear long and slender, have thin, almost transparent walls (C. *OHr*), and are connected with sense cells.

From the preceding it is evident that pore plates, found only on the antennae of aphids, bees, wasps, and on some beetles, are totally absent on the antennae of the Mexican bean beetle. The pore plates,

when present, are considered the olfactory organs by most writers. Figure 7 illustrates the antennal organs of a water beetle, copied from Hochreuther (25). The pore plates (*PP*), hollow pit pegs (*HPPg*), and massive pit pegs (*MPPg*) might be called olfactory organs, but Hochreuther regarded only the hollow pit pegs as probably olfactory in function. If they really act as olfactory organs, then the mouth parts, thorax, legs, and sexual organs must aid in receiving odor stimuli, because Hochreuther found them also on these parts of the anatomy.
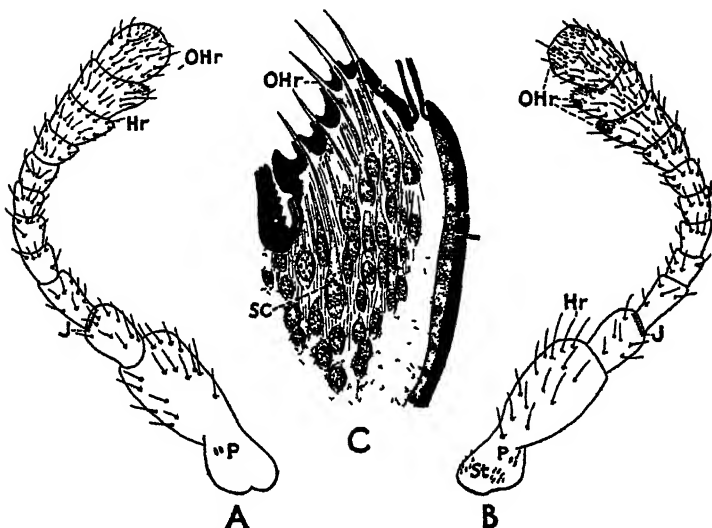
FIG. 6.—Drawings of antennae of adult Mexican bean beetle, showing organs on them. A, ventral surface, and B, dorsal surface, showing location of following: *Hr*, noninnervated hairs; *J*, Johnston organs; *P*, pores called olfactory by the writer; *OHr*, so-called olfactory hairs; and *St*, tactile hairs C, a semidiagrammatic drawing from a section through tenth segment, showing structure of so-called olfactory hairs (*OHr*) and their sense cells (*SC*). A and B, × 53; and C, × 500.

(B) OLFACTORY PORES

The writer (46, p. 1105) in 1926 cited references pertaining to these organs in beetles and in 1929 he (47, p. 27) stated why they were called "olfactory pores." In 1915 (41) he made a comparative study of them in 50 species of beetles belonging to 47 genera and representing 34 families. In that study only the legs, elytra, and wings were examined for these pores. A group of pores (fig. 8, A and B, *1*) was always found on the peduncle of each elytron. The number of pores in it ranged from 12 to 310, and the more pores in the group the smaller they were and the closer they were together. Of the 47
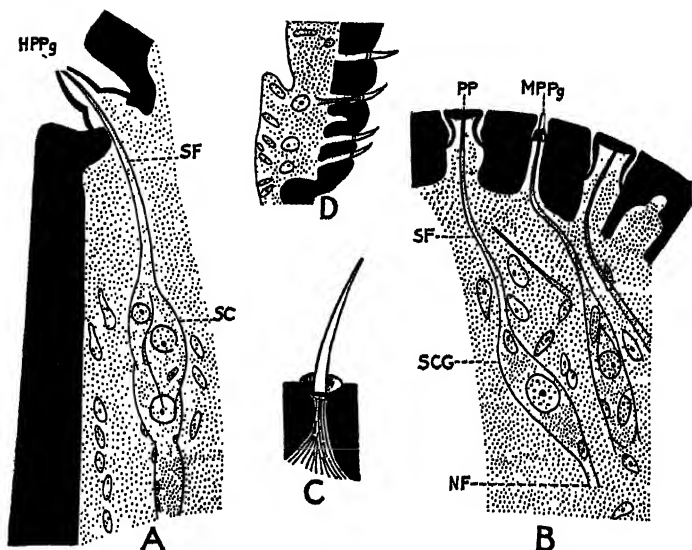
FIG. 7.—Antennal organs of a water beetle, *Dytiscus marginalis*, copied from Hochreuther (*25*). A, longitudinal section through a hollow pit peg (*HPPg*); B, longitudinal section through a small massive pit peg (*MPPg*) and 2 pore plates (*PP*). This drawing is a combination of Figs. 32 and 58 from Hochreuther, slightly modified. C, a small tactile hair from first segment, total preparation; and D, portion of Fig. 12 from Hochreuther, showing 4 small sense bristles from second segment. *NF*, nerve fiber; *SC*, sense cell; *SCG*, sense cell group; and *SF*, sense fiber.
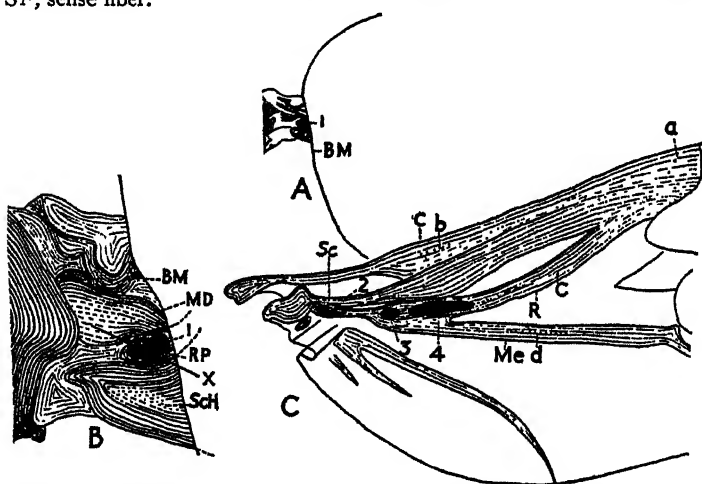
FIG. 8.—Portion of left elytron (A and B) and left wing (C) of Mexican bean beetle, showing position of olfactory pores as indicated by numbers *1* to *4* and letters *a* to *d* on dorsal surfaces. A shows relative sizes of peduncle of elytron and group *1* when compared with size of basal margin (*BM*) of elytron; A and C, × 12; and B, × 67. The lower side of A and B is the outer margin of the elytron. *C*, costa; *MD*, muscle disk; *Me*, media; *R*, radius; *RP*, radial plate; *Sc*, subcosta; *ScH*, subcostal head.

winged species examined, 11 had only one group of pores on each wing, 21 had two groups on each wing, 12 had three groups on each wing (C, *2, 3,* and *4*), and 3 had four groups on each wing. The
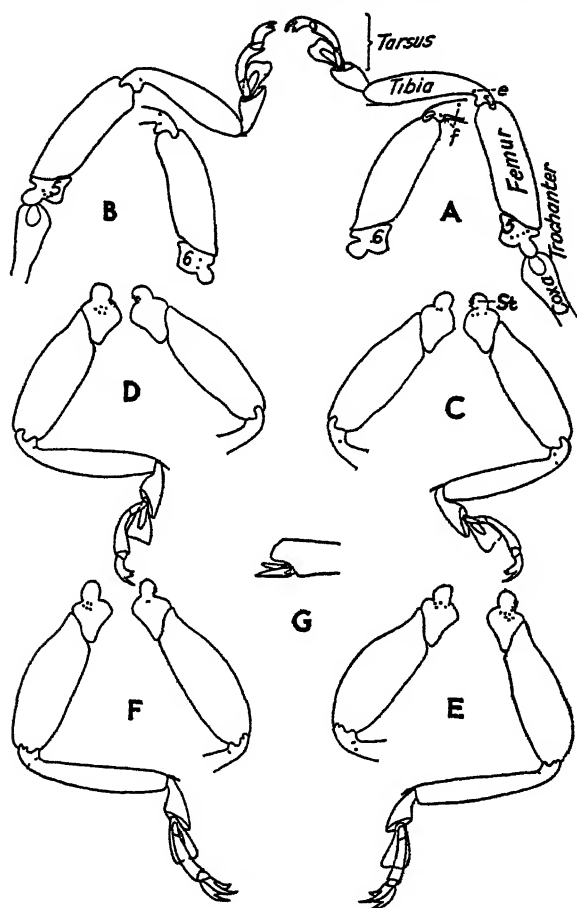
Fig. 9.—Position of sense organs on legs of adult beetles; dots, marked *5* and *6*, and *e* and *f*, being olfactory pores; and *St*, tactile hairs. A to F, legs of Mexican bean beetle, × 12; and G, distal end of tibia from front leg of *Epicauta marginata*, showing *5* olfactory pores on tibial spine. The drawing of each leg in which the tarsus is shown represents the outer surface and the portion of leg without tarsus represents the inner surface of the same leg. A, right front leg; B, left front leg; C, right middle leg; D, left middle leg; E, right hind leg; and F, left hind leg.

number of pores on a pair of wings ranged from 130 to 982. The number of pores counted on all six legs of an individual ranged from 49 to 341. There were usually two groups of pores on each trochanter (fig. 9, *5* and *6*). Sometimes a pore was found at the proximal end of

the femur. A few pores were always found at the proximal end of each tibia (*e* and *f*), and sometimes pores were found in the tibial spines (G) and on the tarsi.

In regard to water beetles, the better the legs are adapted for locomotion in water, the fewer pores they have. The smallest winged species examined had 273 pores, which is the smallest number counted of all the species, and the largest species had 1,268 pores which is the largest number of all the species examined. The wingless species had more pores on the legs than usual. As a rule, the smaller the species, the fewer its pores and the larger they are, comparatively speaking. As a rule, no generic and specific differences were found, except variations in number of pores, the amount of variation depending on the sizes of the individuals compared. There were no individual and sexual differences other than slight variations in number of pores.

The pore apertures or pits are round, oblong, slitlike, or club-shaped. On the elytra and wings (fig. 10, A and B, *Ap*) they are always round or oblong. On the legs (C) they have all four of the enumerated shapes.

The spindle-shaped sense cells (fig. 10, C, *SC*) of most beetles lie in the lumens of the appendages outside the pore cavities. A small chitinous cone (*Co*) is always present. It is formed by the hypodermal cell at the mouth of the pore after the insect has emerged from the last pupal instar, and at the same time when the chitinous integument is being considerably thickened. The sense cells are fully developed when the insect emerges into the imago. The sense fiber pierces the cone, and comes in direct contact with the outside air. This statement is denied by other writers. In the legs of the lady-beetle *Epilachna borealis* the pore apertures lie in the center of domes (fig. 10, C) above the general surface of the legs.

A large nerve and a large trachea run into each elytron (fig. 10, A, *N* and *Tr*) and wing. In the peduncle of the elytron they run through the radial plate just beneath the group of olfactory pores. Branches from the nerve are given off which connect with the sense cells. The large nerve and trachea passing into the wing soon divide so that a smaller nerve and a smaller trachea (B, *N* and *Tr*) run through each main vein. The largest trachea passes through the subcosta, and the largest nerves pass through the veins bearing the olfactory pores. These nerves give off branches which connect with the sense cells. The sense cells (C, *SC*), wherever found, are always surrounded by blood (*Bl*).

In a study of the sense organs of the cotton boll weevil, the writer (46) found the olfactory pores common to both the adult and larva;
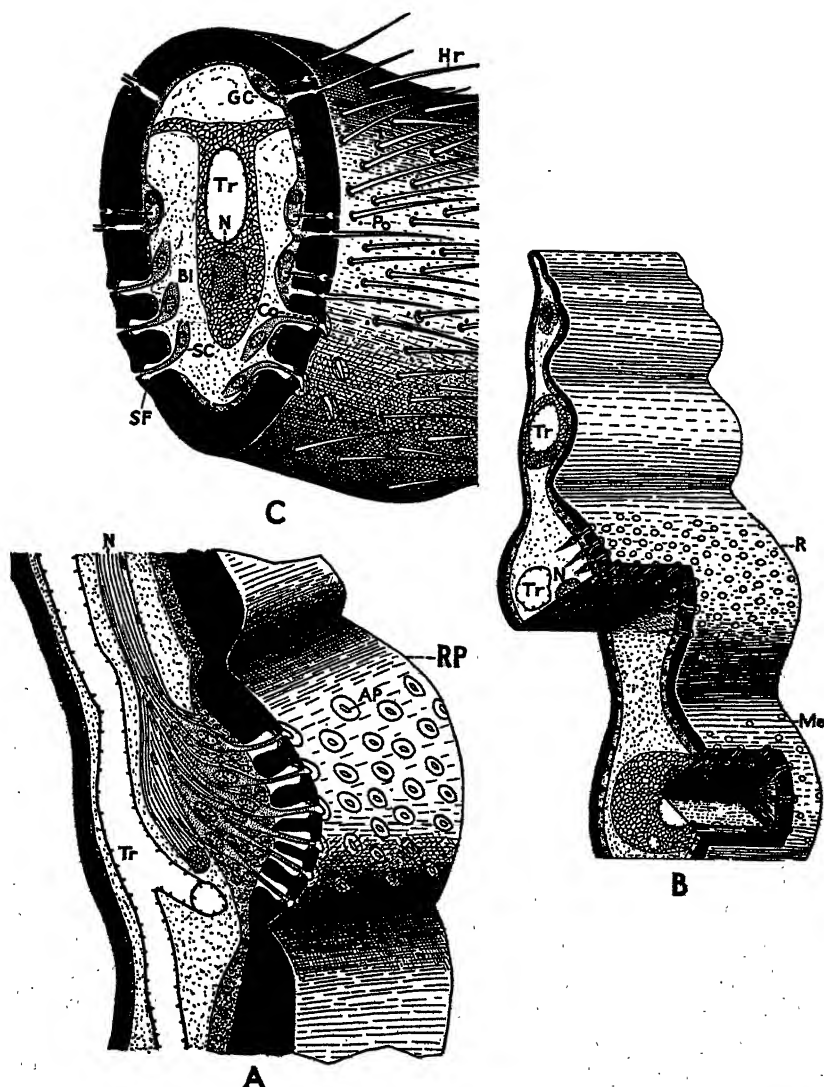
FIG. 10.—Diagrams showing portions of elytron, wing, and leg of adult beetles, to illustrate internal and external anatomy of these appendages and of olfactory pores and hypodermal glands. A, oblique transverse-longitudinal view of portion of peduncle of *Epilachna borealis*. The transverse portion passes through group 1 of the olfactory pores and radial plate (*RP*) in the direction of the line marked X in figure 8 B. B, transverse-longitudinal view of portion of wing of *Orthosoma*, passing through pores on radius (*R*) and media (*Me*). C, transverse-longitudinal view of proximal end of trochanter belonging to right hind leg of *E. borealis*, passing through group 6 of olfactory pores (4 pores on right) and group 5 (3 pores at left). *Ap*, pore aperture, *Bl*, Blood; *Co*, chitinous cone; *GC*, hypodermal gland cell; *Hr*, noninnervated hair; *N*, nerve; *Po*, pore of hypodermal gland; *SC*, sense cell; *SF*, sense fiber; and *Tr*, trachea.

but the other so-called olfactory organs, which are nothing more than ordinary innervated hairs, are common only to the antennae of the adult, although similar innervated hairs are also found on other parts of both adult and larva   In the adult the olfactory pores were found on the head capsules, legs, elytra, wings, and mouth parts, and at the base of the antennae, in the larva, on the head capsule, base of antennae, mouth parts, clypeus, and second thoracic segment   The individual and sexual variations found in the pores were small, although the females have 13 7 per cent more pores than have the males
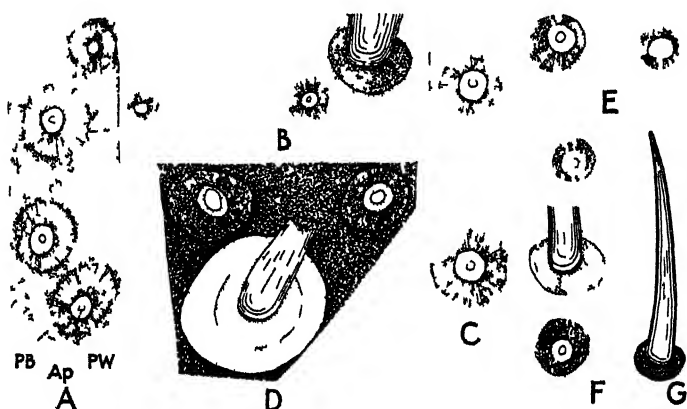
Fig 11 —External view of single olfactory organs and noninnervated hairs on larva of *Cotinis nitida* × 320   A, 4 organs from trochanter, showing pore border (*PB*), pore aperture (*Ap*) and pore wall (*PW*)   B, 2 organs and a hair from hypopleural region, C 2 organs from maxilla, D 2 organs and a hair from labrum, E, 2 organs from labium   F 2 organs and a hair from epicranium and G, a hair from first antennal segment

On the larva of the green June beetle (*Cotinis nitida* L) the writer (44) found the olfactory pores unusually numerous and consisting of two types   The single olfactory organs are isolated pores, not arranged in groups   They were found on the antennae, all mouth parts, head capsule, thorax, and legs, and average 1,359 pores per individual larva   This number is slightly more than the total number of pores found on the elytra, wings, and legs of an adult of the same species   Their external anatomy is unusual in that the pore border (fig. 11, *PB*) is radially striated, while the border around the hairs never shows striae   The compound olfactory organs (fig 12) are variously shaped plates, each of which bears many apertures. They were found only on the distal halves of the last antennal segments. Figure 13 illustrates the internal anatomy of the single and compound organs
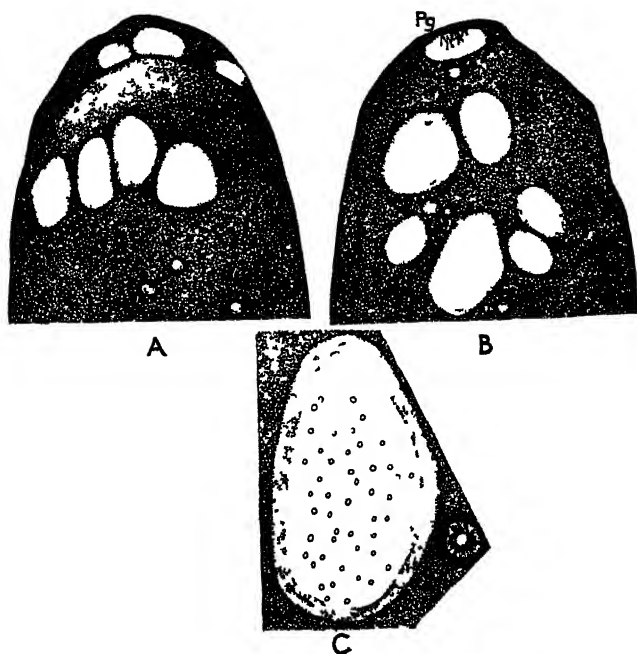
FIG 12 —External view of compound and single olfactory organs and olfactory pegs on distal half of last antennal segment of larva of *Cotinis nitida*. A, 9 compound organs and 3 single ones on ventral side of antenna, viewed from a flat surface, $\times$ 100, 2 of the compound organs at extreme tip are not shown. B, 6 compound organs, 4 single ones, and 1 group of olfactory pegs (*Pg*) on dorsal side of antenna, viewed from a flat surface, $\times$ 100. C, external view of a compound and a single organ, $\times$ 320, the small circles represent pore apertures
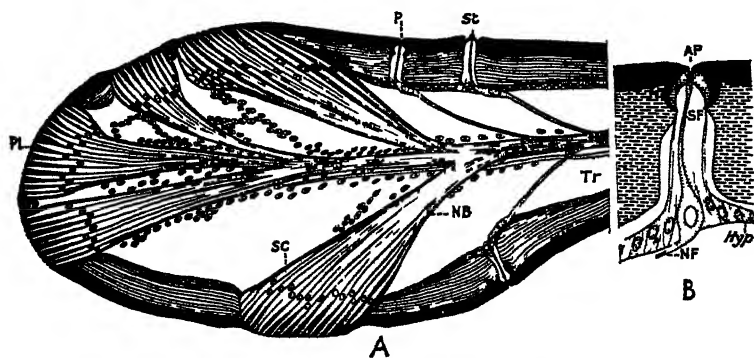
FIG. 13 —Internal anatomy of sense organs on antenna of larva of *Cotinis nitida*. A, longitudinal section through tip of antenna, showing innervation of compound (*Pl*) and single olfactory organs (*P*), and tactile hair (*St*); two-thirds diagrammatic, $\times$ 100. (At this magnification the pore apertures are never discernible). B, cross section through single olfactory organ from antenna, $\times$ 500. *Ap*, pore aperture; *Hyp*, hypodermis: *NB*, nerve branch; *NF*, nerve fiber; *SC*, sense cell; *SF*, sense fiber; and *Tr*, trachea.

The olfactory pores on several males and females of the Mexican
bean beetle were examined, but they were actually counted on only
one female, and these are illustrated in figures 6, 8, 9, 14, and 15. In
this study only one totally new fact was learned. In all the previous
studies on beetles, no olfactory pores were seen on the ventral side of
the peduncles of the elytra, but in this position on the bean beetle 7
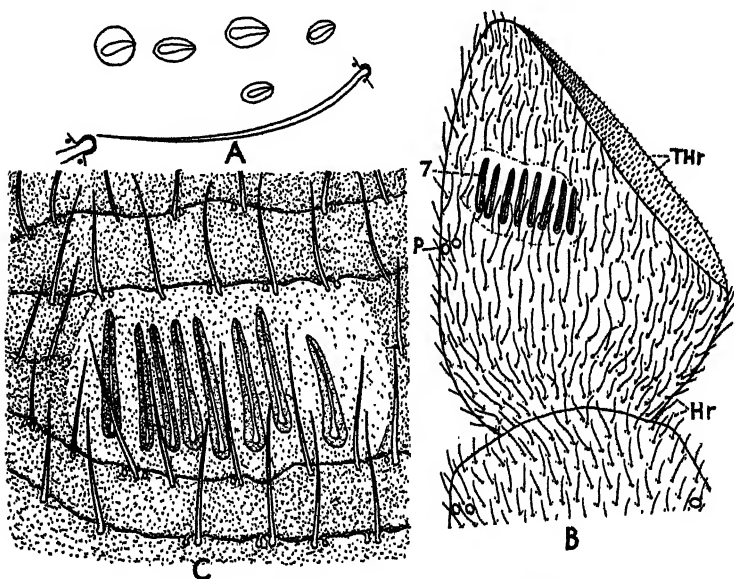pores were seen on one elytron and 6 pores on the other. The groups

FIG. 14.—External view of chemoreceptors of adult Mexican bean beetle. A,
noninnervated hairs and group 5 of olfactory pores on trochanter of front leg,
× 500. B, ventral surface of distal end of maxillary palpus, showing numerous
noninnervated hairs (Hr) with their gland pores, isolated olfactory pores (P),
group 7 of olfactory pores (7), and a plate bearing numerous so-called taste
hairs (THr), × 100. C, group 7 of olfactory pores, markings on chitin, hairs,
and gland pores, × 500.

of pores are numbered, as usual, from 1 to 7, and small letters are
used to indicate the position of some of the isolated pores. Group 1
on the elytra (fig. 8, A) contains 58 pores on the left peduncle and
65 on the right one. Groups 2, 3, and 4 on the dorsal surface of the
wings (C) have as follows: Group 2, 58 and 64 pores; group 3, 43
and 38 pores; and group 4, 70 and 64 pores. Isolated pores on the
wings are as follows: At a, 2 on the ventral side; at b, 8 on the dorsal
side; at c, 1 on the dorsal side; and at d, 12 on the dorsal side and 8
on the ventral side. The number of pores in groups 5 and 6 and at e

and f on the legs (fig 9) can be counted by inspection Group 7, consisting of 8 slit shaped pores lies on the ventral surface of the terminal segment of the maxillary palpus All the remaining pores counted are isolated ones found on the antennae and mouth parts The total number of pores on all appendages of the same bean beetle are as follows Wings 397, elytra 136 legs 95 maxillae 32, labium 14, antennae 8, mandibles 6, and labrum 4, making 692 in all The
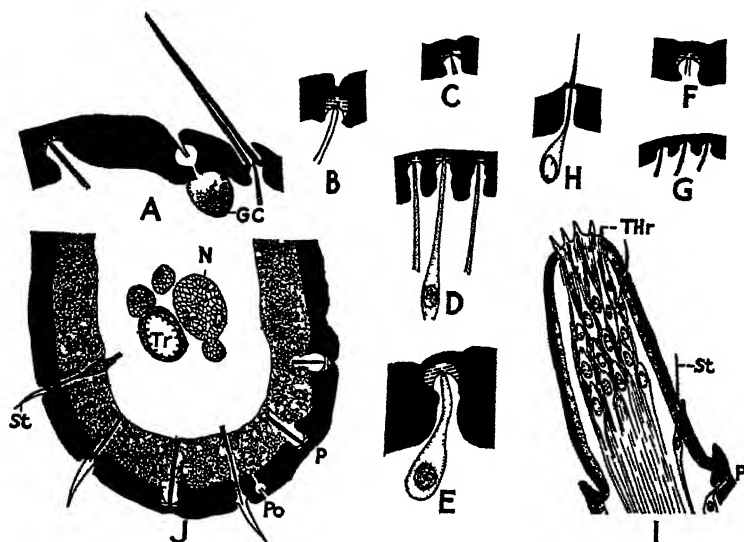

FIG 15 —Internal structure of sense organs on adult Mexican bean beetle, × 500 A, an olfactory pore, gland cell (*GC*), and sense hair from dorsal surface of labrum B to G, olfactory pores B from mandible C, from maxilla D from elytron, E, from trochanter F from tibia and G from wing H sense hair from trochanter I drawing two-thirds diagrammatic from longitudinal sections of distal end of labial palpus, showing innervation of so called taste hairs (*THr*), tactile hairs (*St*), and olfactory pore (*P*) J, semidiagrammatic drawing from 3 cross sections through base of first antennal segment showing tactile hairs (*St*), gland pore (*Po*) olfactory pore (*P*), trachea (*Tr*), and nerve (*N*)

fact that this number is small for an adult insect might be correlated with the fact that the bean beetle is " stupid ' when the olfactory responses are considered

The olfactory pores on several individuals of all four instars of bean-beetle larvae were examined Since no differences in number and position were observed, the pores were carefully studied on only individuals of the fourth instar They are illustrated in figure 16 The total number of pores on all appendages and the head are as follows: Legs 30, maxillae 12, head capsule 6, antennae 4, labrum 4,

labium 4, and mandibles 2, making 62 pores in all. The fact that this number is extremely low for any insect may help to explain why these larvae did not respond readily to odor stimuli.
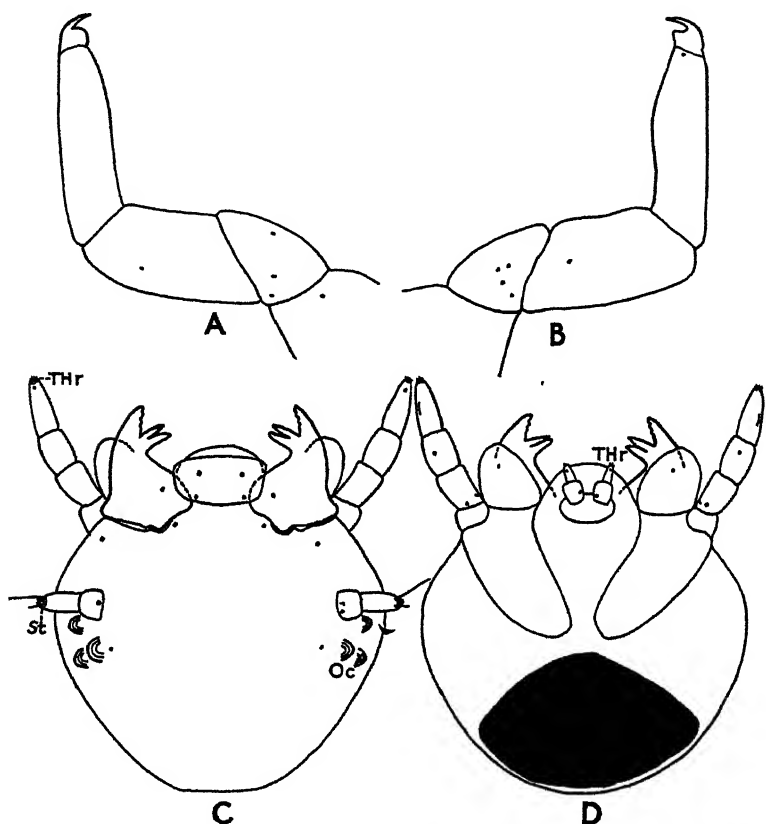

FIG. 16.—Position of olfactory pores (dots), 12 to 15 so-called taste hairs (*Thr*) at tip of each maxillary palpus, 8 tactile or so-called olfactory hairs (*St*) at tip of each antenna, and ocelli (*Oc*) on larva of bean beetle, × 32. A and B, inner and outer sides respectively of right front leg. The number of pores on the legs is nearly constant, and they shift only slightly in position. C and D, dorsal and ventral surfaces respectively of the head and head appendages. On the base of each antenna one pore is on the dorsal side and one on the ventral side. On each terminal maxillary segment there is a slit-shaped pore.

2. SO-CALLED TASTE ORGANS

Several writers, particularly Nagel (58), have described certain tiny peglike hairs on the mouth parts of insects as taste organs, but no one has ever demonstrated that they perform such a function. Hochreuther (25) found many "Tast- und Geschmackszäpfchen" on the maxillary and labial palpi of the water beetle *Dytiscus margi-*

nalis. The earlier papers concerning the chemoreceptors of Coleoptera are reviewed by Deegener (see Schröder (72, pp. 150-151). Since Minnich's papers on the taste organs of butterflies and flies have recently been reviewed by the writer (47, pp. 36-39), they will not be discussed here. The reader should know, however, that according to the experiments conducted by Minnich certain butterflies bear so-called taste organs in their tarsi, and certain hairs on the proboscis of the blowfly serve as gustatory organs. The most recent paper by Minnich (55) discusses the chemical sensitivity of the legs of a blowfly.

The writer (46) described and illustrated many tiny peglike hairs found on the cotton boll weevil, but did not attribute a gustatory
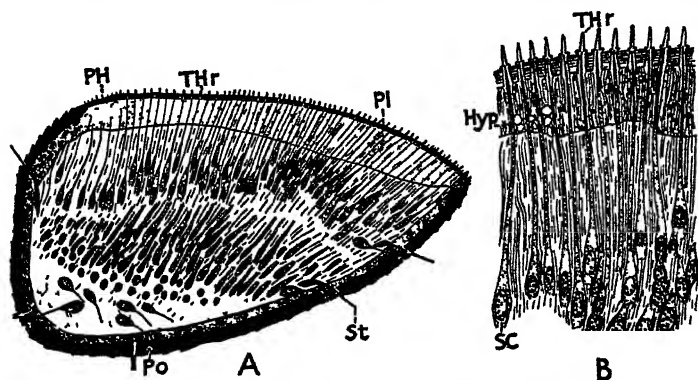
Fig. 17.—Internal anatomy through tip of maxillary palpus of adult Mexican bean beetle, showing following: *Hyp,* thick hypodermis; *PH,* pseudohairs; *Pl,* soft plate; *Po,* gland pore connected with gland cell, which lies some distance from pore; *SC,* sense cells; *St,* tactile hairs; and *THr,* so-called taste hairs. A, drawing, two-thirds diagrammatic, × 300; and B, semidiagrammatic, × 500

function to any of them. According to position, and possibly to struc-ture, the ones on the tips of the labial and maxillary palpi are best suited to be taste organs. The same type of hairs was also found at the same place on both adult and larva of the Mexican bean beetle (figs. 14-17, *THr*). The ones at the tip of the maxillary palpus of the adult (fig. 14, B) are the most numerous and most conspicuous of any yet observed by the writer, and consequently they would appear to have some function other than that of touch. These tiny, thin-walled, and transparent hairs arise from a slightly convex plate, which is soft, flexible, and transparent. The number of hairs on the organ illustrated in figure 17 is about 447. An oblique cross section through the fourth or terminal maxillary segment is represented by figure 17,

5

A. The transparent plate (*Pl*) is bordered by tiny pseudo-hairs (*PH*) and the hypodermis (B, *Hyp*) just beneath the plate is very thick. Each hair is connected with a sense cell (*SC*) and these cells almost fill the lumen of the segment. The sense cells are very long and slender, and have conspicuous nuclei.

Now, if aqueous solutions can pass quickly through the walls of these sense hairs in order to stimulate the nerves inside, these structures would be excellent taste organs. Or, if air can pass quickly to the nerves, they would then be olfactory organs. The fact that the bean beetle possesses two of these highly developed sense organs helps to explain how these insects were able to distinguish so readily between the various aqueous solutions and insecticides fed to them.

III. AUDIRECEPTORS

Since the writer (46, p. 1119; 47, p. 39) has already reviewed the literature on the sense of hearing in insects, no further review is necessary here, other than to cite the recent book by Eggers(14).

1. JOHNSTON ORGANS

In caustic-potash preparations of the antennae of the adult bean beetle the location of the Johnston organs may be determined by focusing downward with the microscope when looking at the distal end of the second antennal segment. A serrated structure (fig. 6, A and B, *J*) will be observed to encircle the segment. The distal ends of the sense cells are attached to this structure. In longitudinal sections the Johnston organs appear about as shown in figure 18, A. At the base of the second segment the nerve divides into two branches, which run directly to the sense cells (*SC*). Formerly the Johnston organs were assumed to be auditory in function, but more recently they have been called muscular receptors or statical-dynamic organs to register the movements of the antennae.

2. CHORDOTONAL ORGANS

Chordotonal organs very often accompany the Johnston organs, as illustrated by the writer in the cotton boll weevil; but none was found in the Mexican bean beetle. Many sections through the larvae were also made and studied, but no chordotonal or Johnston organs were found.

Since the writer has never reviewed the literature on the so-called auditory organs in larvae, the reader is referred to the paper by Hess (24) who gives a brief history of the chordotonal organs and de-

scribes them in cerambycid larvae. Hess determined that the pleural discs in these larvae are the points of attachment of abdominal chordotonal organs. Two of Hess's drawings (fig 18, B and C) were copied to illustrate the internal structure of these organs in coleopterous larvae.
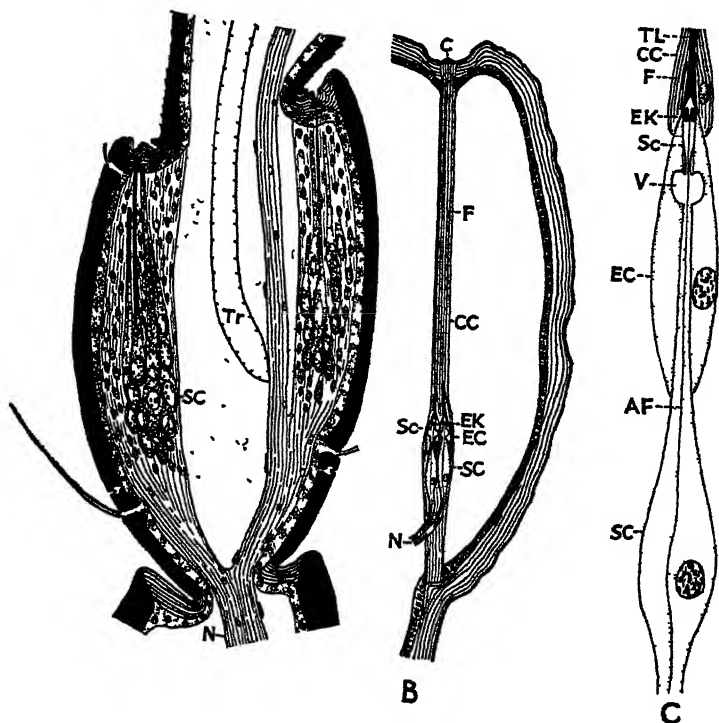

FIG. 18—Internal anatomy of so-called auditory organs of beetles. A, drawing, two-thirds diagrammatic, from longitudinal sections through second antennal segment of an adult Mexican bean beetle, showing Johnston organs consisting of groups of sense cells (*SC*), × 500. B and C (after Hess), longitudinal-vertical section of the pleural zone and chordotonal ligament from a larva of *Ergates spiculatus*, showing following: *AF*, axis fiber; *C*, chitinous cap; *CC*, cap cell; *EC*, enveloping cell, *EK*, end knob; *F*, fibrils of cap cell; *N*, chordotonal nerve; *Sc*, scolopale; *SC*, sense cell, *TL*, terminal ligament; and *V*, vacuole

IV. THIGMORECEPTORS

I. TACTILE HAIRS

Hochreuther (25) made a thorough study of the sense hairs on a water beetle (*Dytiscus marginalis*). On the basis of external structure, he separated them into five divisions. Vom Rath (63, 64) found sense cells connected with all the small hairs on the maxillary palpi of *Coccinella septempunctata, Melolontha vulgaris,* and *Tenebrio*

molitor, and also with all the small hairs on the labial palpi of the last species. The present writer (46) found tactile hairs on the cotton boll weevil as follows: Sense hairs (Sensilla trichodea) on the head capsule, antennae, mouth parts, thorax, legs, wings and abdomen; sense bristles (S. chaetica) on nearly the same parts; and sense pegs (S. basiconica) on the head capsule, mouth parts, and genitalia.

In regard to tactile hairs on the Mexican bean beetles, all parts of the integument were not searched for them, but practically all the innervated hairs already discussed might be considered as touch hairs; however, the sense hairs (Sensilla trichodea) are considered to have no function other than that of touch. On the base of each antenna lie two groups of these hairs (figs. 6, B, and 15, J. *St*) and each trochanter bears one or two groups (fig. 9, C, and 15, H, *St*). They were also found on the maxillary and labial palpi (fig. 15, I, *St*) of the adult and on the head (fig. 16, C, *St*) of the larva.

C. Scent-Producing Organs and Reflex " Bleeding "

The study of scent-producing organs follows as a corollary to that of tropisms and sensory receptors, and reflex " bleeding " is closely related to them. Since the sense of smell is such an important means of communication among insects, it is probably true that all insects have structures for producing odors. In fact these structures have already been described for most insect orders, and particularly for Coleoptera.

The writer (43) in 1917 reviewed the literature on this subject. A brief summary of that review concerning beetles follows: The simplest type of a scent-producing organ in beetles is composed of unicellular glands distributed over the entire body surface. In some beetles these unicellular glands are grouped and thus form glands varying considerably in complexity. In *Malachius* two pairs of caruncles serve as the scent-producing organs; unicellular glands lie in the walls of these structures. In *Dytiscus, Gyrinus,* and *Acilius* two different kinds of liquids issue from unicellular glands situated in the articular membranes between the thoracic segments. The liquid emitted at the femoro-tibial articulation during reflex " bleeding " of certain beetles seems to be secreted by two types of unicellular glands at this location. The highest type of scent-producing organ among insects is the anal glands of beetles. These have been found in several families.

In regard to the Mexican bean beetle, no careful search was made for the purpose of finding scent-producing organs other than the

unicellular glands distributed over the entire body surface. In fact this type of scent organ is the only one in lady-beetles known to the writer. The bean beetle, like other coccinellids, is well supplied with these glands. All parts of the body surface are covered with comparatively large hairs. Near the base of each hair there is usually one and sometimes two gland pores (figs. 6, 10, 14, 15, 17-19, *Po*). The large gland cells (figs. 10, C, and 15, A, *GC*) are variously constructed, but are always connected with reservoirs lying in the integument. In some of the smaller appendages, for example the maxillary palpi, where the available space is limited, the gland cells lie some distance from their pores and often nearly fill the lumen of the appendage.   .

The writer (42) in 1916 reviewed the literature on reflex " bleeding " in beetles and added further information by using the squash lady-beetle, *Epilachna borealis*. When disturbed certain coccinellid and meloid beetles fold the antennae and legs against the body, eject small drops of liquid from the femoro-tibial articulations, and feign death. There has been a controversy as to how the liquid is expelled so quickly and as to whether the liquid is blood or is a glandular secretion. The writer has now shown that in regard to the squash lady-beetle and the Mexican bean beetle (*E. corrupta*) the phenomenon is a true reflex, but that instead of the liquid being blood, it is a secretion from two types of hypodermal glands and that it passes to the exterior through innumerable tubes opening near and in the articular membrane. The gland pores of the first type, with reservoirs, lie in groups on the tarsi and around the femoro-tibial articulations. Two groups of these are located at the extreme proximal end of the tibia and two at the distal end of the femur around the articular membrane (fig. 19, A, *Po*). The gland pores of the second type, without reservoirs, lie in the articular membrane, marked *a* in figure 19. The discharge of the amber-colored secretion is accomplished by putting the gland cells under a high blood pressure. This is made possible by a muscular contraction in the femur whereby the blood is forced into a specially devised chamber containing the gland cells which belong to the pores in and near the femoro-tibial articulation. The glandular secretion is bitter and has an offensive odor. Its chief purpose is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species.

Hollande (26) in 1911 wrote a large paper in which he reviewed the literature on the phenomenon of discharging " blood " in insects and on the toxicity of this substance. He also added new information on these subjects. He reports that self-bleeding has been found in

Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. Under his general conclusions he states that some authors believe that the discharged liquid is blood, while others think it is a glandular secretion. The manner in which the liquid is discharged is little known, except in a few cases. In general it is admitted that the blood is discharged by a reflex action, being a means of defense. He discusses four methods in which the blood is discharged and gives
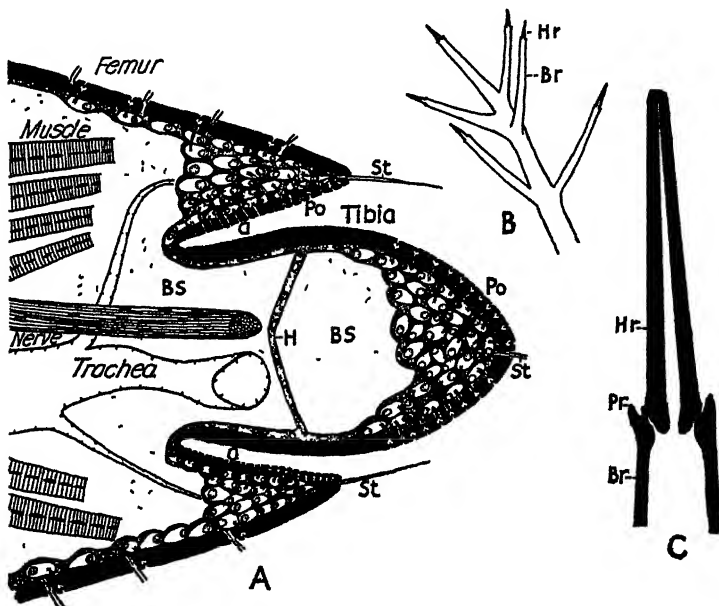

Fig. 19.—Drawings, illustrating reflex "bleeding" in lady-beetles. A, diagram of a section through femoro-tibial articulation of *Epilachna borealis*, showing following: *a*, pores of gland cells without reservoirs; *BS*, blood sinus; *H*, membrane dividing lumen of leg into two chambers; *Po*, pores of gland cells having reservoirs; and *St*, sense hairs. B and C, portion of tubercle on larva of bean beetle; B, distal end of tubercle having 6 branches (*Br*), each of which is terminated with a hair (*Hr*), × 32; and C, distal end of a branch, showing hair arising from a socket, which is surrounded by 5 processes (*Pr*), only 2 being shown, × 320.

examples of insects for each method. He further remarks that the ejected blood is usually very toxic.

While discussing coleopterous larvae, Hollande shows how coccinellid larvae protect themselves by discharging blood. As an example he used *Epilachna argus*, whose body is covered with chitinous tubercles, which in turn bear many smaller branches, each of which is terminated by a hair. The discharged blood is accomplished by a rupture of the chitin near the base of the hair. When one seizes the

larva with the fingers, the hairs pierce the epidermis on the fingers and are then broken off, causing the blood of the larva to exude as small drops.

The larvae of the bean beetle are likewise covered with hairlike tubercles (fig. 19, B), which bear many branches (*Br*), each of which is terminated by a hair (*Hr*). While picking up the larvae the writer observed a yellowish liquid on his fingers. This liquid was bitter and very distasteful. After carefully examining the larvae under a binocular, it was learned that the bitter liquid came from the tips of the branches (C, *Br*). Using a needle it was possible to touch the hairs (*Hr*) lightly, so that they broke at their weakest point; that is, at the socket which is surrounded by five processes (*Pr*).

SUMMARY

This paper is written as a complement to the writer's (47) former one entitled " Tropisms and Sense Organs of Lepidoptera," and contains information of a similar nature, but dealing with Coleoptera alone. A large mass of literature on the sense organs and tropisms of beetles, including papers on light traps, attractive baits, and repellents, has been consulted; but only the more important information found has been briefly summarized.

The Mexican bean beetle was selected to represent the Coleoptera. When tested to odor stimuli alone this beetle was found to be an unfavorable insect; but when the adults were allowed to come in contact with the substances to be tested as foods, the beetles clearly demonstrated their " likes " and " dislikes "; and when tested to light and gravity in a dark-room, the adults proved to be almost ideal for this purpose. In order to obtain comparative results which could be treated statistically, new technique and apparatus were devised, and the more important experiments were repeated many times under controlled conditions. The more important results obtained are as follows:

When tested in a phototactic box, which lay on a table by a south window in bright light, although not in direct sunshine, larvae of the first and second instars were weakly photopositive or indifferent to light. Most of the larvae of the third instar and the more active ones of the fourth instar were strongly photopositive. As a rule, the larvae up to the time of pupation were found to be photopositive, but when ready to pupate they became photonegative. Whether the negative reaction is caused by a change in the structure of the ocelli is not known. Hundreds of adult bean beetles were also tested and all proved to be photopositive, most of them being strongly so.

In a dark-room in which the temperature and relative humidity were fairly constant many tests were conducted to determine the difference between the phototactic and geotactic responses of adult bean beetles and their larvae, with and without the use of light. The insects were confined in a photo-geotactic box, just above or below which lay a water screen to prevent the infra-red or heat rays from reaching the beetles. Under these conditions the following results were obtained. For active, overwintering adult beetles the geonegative or upward response, when light was used, was 25.6 ± 0.20 per cent stronger than the geopositive or downward one; but when no light was used, it was 54.6 ± 0.17 per cent stronger, indicating that when the beetles were forced downward by the light this stimulus overcame about one-half of the geotactic one. Old beetles of the second brood did not respond so readily, yet their geonegative responses were stronger than their geopositive ones. Larvae of the third instar did not respond readily and they went up only slightly more than down. When light was used, active larvae of the fourth instar reacted as readily as did the overwintering adults; but when no light was used, they did not respond so readily, although they went up more than down.

While searching for attractants and repellents an improved feeding method was devised. The adult bean beetles were confined in four small wire-screen cages, each of which contained a row of the same four foods, but differently arranged. This series of tests, with the foods differently arranged each time, was then repeated three times in the forenoon, and usually the four series were again repeated in the afternoon. Each individual food used was therefore tested 16 times in the forenoon and usually 16 times in the afternoon. According to the arrangement of food, no two rows in the same cage were exactly alike; likewise, no two rows of all 16 rows were identical, although the distribution of food was not so complete. This plan was adopted in order to equalize the number of beetles counted on the same food which lay in all four positions during any one series of tests; and furthermore, everything possible was done to obtain reliable data which could be treated statistically. Using this plan the following results were obtained.

To determine whether bean beetles " like " or " dislike " the four classes of substances which produce the four human attributes of taste, many series of tests were conducted. It was soon learned that they have " likes " and " dislikes " in regard to food. They " disliked " water containing salts, acids, bitter materials, and saccharine; but " liked " the other sweet substances tested, including cane sugar,

grape sugar, table molasses, corn sirup, and black-strap molasses, and even showed preferences between them.

Bean foliage, sprayed with arsenicals, was repellent, but not sufficiently so to prevent the leaves from being eaten. Lead arsenate was most repellent; magnesium arsenate was less so; and calcium arsenate was least repellent. Bean foliage sprayed with sweetened arsenicals was more attractive than unsprayed foliage. Bean foliage sprayed with sweetened magnesium arsenate was more attractive than foliage sprayed with nonsweetened magnesium arsenate. This would indicate that it might be of economic importance to use sweetened arsenicals in control measures, particularly to poison the overwintering beetles early in the season.

In regard to the tropic receptors of the bean beetle, the following may be stated. The structure of the compound eyes and ocelli was not studied, but these organs are normally developed and seem to function adequately, so far as beetles are concerned.

Two kinds of so-called smelling organs—certain hairs on the antennae, and pores, called olfactory by the writer—are fully described. These hairs appear long and slender, have thin, almost transparent walls, and are connected with the sense cells. They are numerous and lie in five groups on the distal ends of the ninth, tenth, and eleventh segments. The olfactory pores on the adult beetle were found as usual on the elytra, wings, legs, mouth parts, and antennae. The total number counted was only 692. The pores on the larva lie on the head, antennae, legs, and mouth parts. The total number found was only 62. The fact that the total number of pores on both adult and larva is comparatively small might be correlated with the fact that this species is " stupid " when olfactory responses are considered.

A so-called taste organ was found at the tip of the maxillary palpus of the adult. It is a soft plate which bears about 447 tiny, thin-walled sense hairs. The fact that the bean beetle possesses two of these highly developed sense organs helps to explain how these insects were able to distinguish so readily between the various aqueous solutions and insecticides fed to them.

The only so-called auditory organ found in the bean beetle lies in the second antennal segment. These structures, called Johnston organs, were formerly assumed to be auditory in function, but now are believed to be muscular receptors to register the movements of the antennae.

The remaining receptors described are the tactile hairs, which are widely distributed over the surface of the beetle.

In connection with the receptors the scent-producing organs and the phenomenon of reflex "bleeding" were studied. The only scent-producing organ found was the unicellular glands, which are distributed over the entire body surface. The bean beetle, like other coccinellids, is well supplied with these hypodermal glands. The chief purpose of the secretion is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species. When disturbed the adults eject small drops of a glandular secretion from the femoro-tibial articulations. This is called reflex "bleeding." The larvae of the bean beetle also protect themselves in a similar manner. When they are handled or even touched the yellowish and bitter "blood" exudes from ruptures at the bases of the hairs, which terminate the branches on the tubercles.

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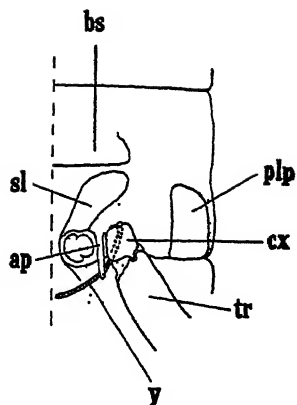1915. The olfactory sense of Coleoptera. Biol. Bur. Mar. Biol. Lab. Woods Hole, 28:407-460, 3 figs., 2 pls.

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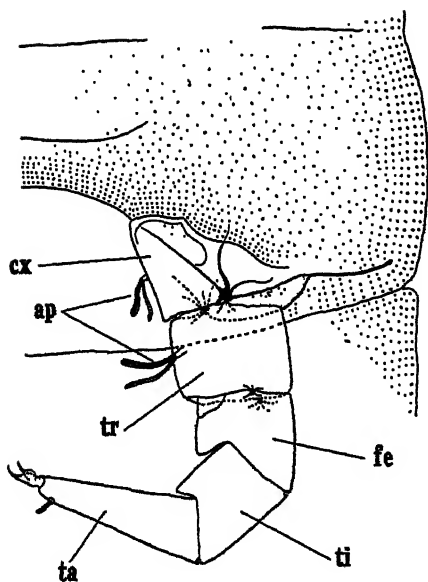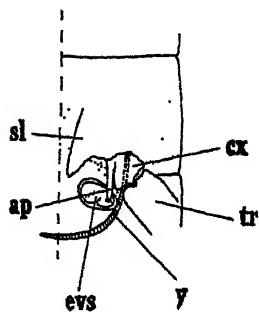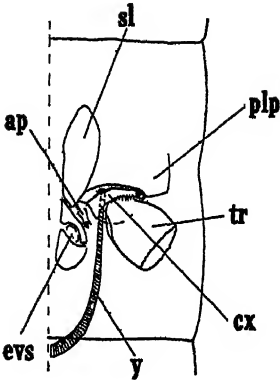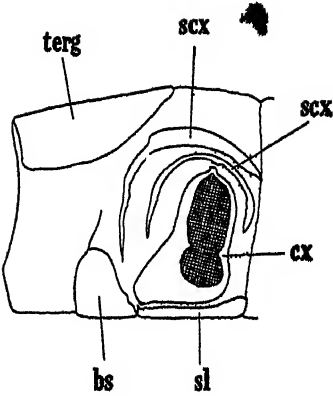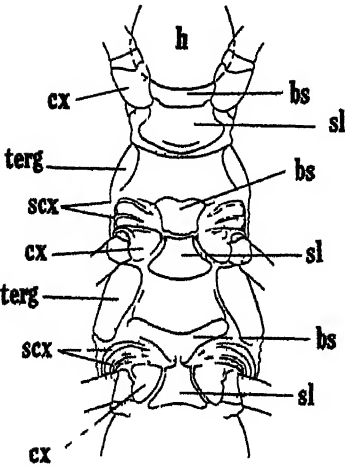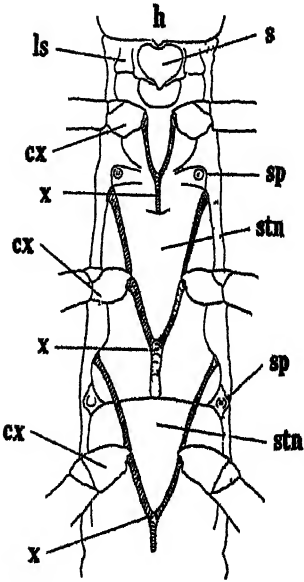
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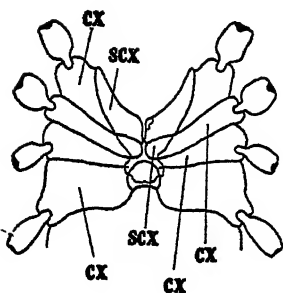
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